TAXONOMIC STATUS OF RED MULBERRY (*MORUS RUBRA,* MORACEAE) AT ITS NORTHWESTERN BOUNDARY

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ABSTRACT

Morus rubra, commonly known as red mulberry, is rare in many areas of its native range in the United States. Previous studies have conflicting reports about the occurrence of *M. rubra* at its northwestern boundary. The main objectives of this study were to determine the northwestern boundary of the native *M. rubra* and provide diagnostic features through analysis of herbarium records, field observation and molecular data. We studied herbarium specimens housed in the major regional herbaria, conducted field studies in Iowa, Kansas, Minnesota, South Dakota and Wisconsin, and analyzed nuclear and chloroplast DNA sequences. We found no occurrence of *M. rubra* in Minnesota and South Dakota. We also did not find *M. rubra* trees in some counties of Nebraska and Iowa as reported earlier. Herbarium records augmented by the nuclear ITS and chloroplast *trnL-trnF* DNA sequences indicated that previous reports were perhaps the results of misidentification that stemmed from introgressive hybridization of *M. rubra* with morphologically similar, but phylogentically, non-sister *M. alba*. In the majority of cases, *M. rubra* identification was mistaken for exotic invasive *M. alba* or hybrid individuals. The results from this study have clarified the geographical range of *M. rubra* near its northwestern boundary and provided salient features for identification of the two species. This information would have implications in developing conservation/management plans for the rare red mulberry in the Midwest United States.

Keywords

Red Mulberry, ITS, *trnL-trnF*, *Morus* identification, Herbarium specimens, Hybridization

INTRODUCTION

Morus L. (Family Moraceae) is a genus of approximately 13 species distributed in Asia, Africa, North, Central and South America (Nepal 2008). Considerable taxonomic confusion exists regarding proper identification of two species of *Morus*: *M. rubra* L. and *M. alba* L. that occur in eastern North America. *M.*

rubra is one of the two native species of mulberries in the United States, the other being *M. microphylla* found in Texas, Arizona and New Mexico (Nepal and Ferguson 2012; Nepal et al. 2012). *M. rubra* occurs from the Atlantic coast to the eastern edge of the Great Plains, south to southern Florida and north to southwestern Ontario in Canada. *M. alba*, the native of China, introduced during colonial times for the silk industry, now occurs as naturalized and invasive throughout the range of *M. rubra* (Wunderlin 1997). The native *M. rubra* occurs mostly in riparian areas, and is considered rare and threatened in many areas including northeastern United States and southeastern Canada (Ambrose and Kirk 2004; Penskar 2009; USDA 2012). The introduced *M. alba* occurs both in forested and open areas and is also cultivated. The two species are known to hybridize where they co-occur (Burgess et al. 2005; Nepal 2008). *M. alba* is potentially posing a threat to the existence of *M. rubra* because of the rapid range expansion, aggressive growth patterns, and reproductive advantages over *M. rubra* (Burgess *et al*. 2005; Nepal 2008). The native *M. rubra* is currently considered endangered in Canada, and in the USA, the states of Connecticut and Massachusetts as well as threatened in Michigan and Vermont (Sullivan 1993; Nepal 2008; USDA 2012).

Previous studies have conflicting reports about the occurrence of *M. rubra* at its northwestern boundary. We encountered several instances of incorrect identification of *Morus* specimens housed in major regional herbaria. The USDA PLANTS distribution map shows the occurrence of *M. rubra* in South Dakota and Minnesota conflicting with the *Morus* description in The Flora of North America (Wunderlin 1997) and the authors' experience. This disagreement might have stemmed from the taxonomic confusion of the two species among the general public as well as some botanists (Nepal et al. 2012). *Morus* identification is often based on highly variable morphological characters of the leaf (*M. rubra*: 5-40 x 3-28cm and *M. alba*: 2-20 x 1.5-18cm) and fruit color which can further complicate the identification process. Currently, it is not clear to many taxonomists whether the species occurs in northern Nebraska, South Dakota, northwestern Iowa, and Minnesota. The objectives of this project were to a) determine the northwestern boundary of the native *M. rubra* in the United States using field data, herbarium records and molecular evidence, and b) assess the morphological differences between the two species. The results would serve primarily as an aid to proper identification of the native *M. rubra* which would have implications in developing conservation/management plans.

METHODS

***Study of Morus herbarium records and field survey*—**We examined over 400 herbarium specimens available in the major Midwest regional herbaria (ISC, ISTC, KSC, MINN, MO, NEB, SDC). Herbarium acronyms followed Index Herbariorum (Holmgren et al. 1990). We conducted field studies of 29 populations: 13 in Kansas from 2005-2007 and, an additional 16 populations in Iowa (five), Minnesota (two), Nebraska (five), South Dakota (three) and Wisconsin (one) in the summers of 2010 and 2011. Consultation with local expert botanists and herbarium specimen locality information were used as a guide to deter-

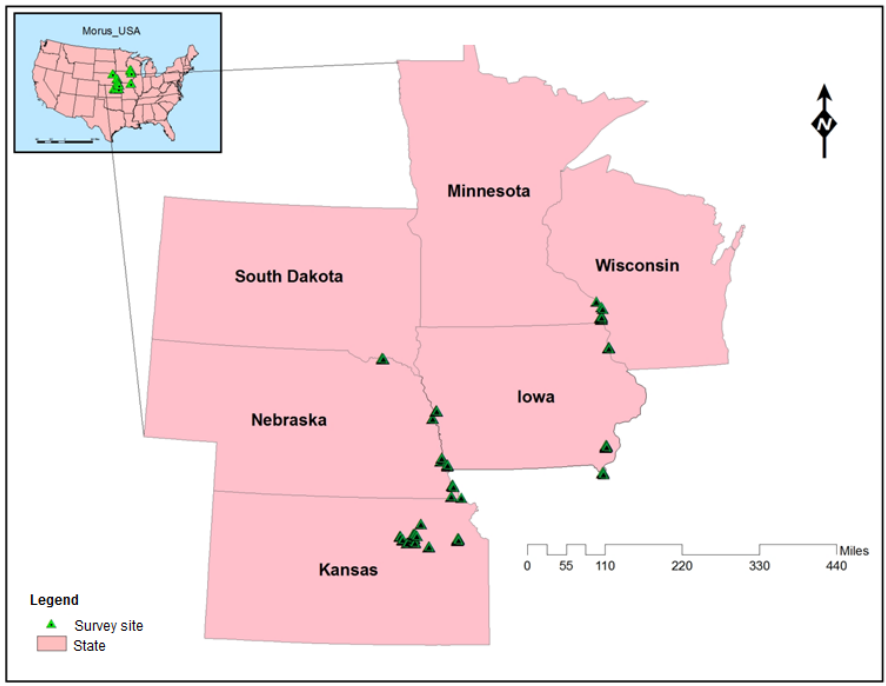

Figure 1. Field survey sites in Iowa, Kansas, Minnesota, Nebraska and South Dakota.

mine our field sites (Figure 1). The GPS coordinates collected in the field were used to construct a field site map using ArcGIS (ESRI 2008). Morphological characters of the bud (size, bud-scale banding), leaf (base, petiole, hair distribution, size, venation, margin and apex), inflorescence (shape, size, number and type of unisexual flowers), style (length) and infructescence (shape, size, color) were used for species identification and description in the field.

***DNA isolation, PCR amplification and sequencing*—**To assess DNA sequence variation among some of the incorrectly identified specimens, we obtained leaf samples of *M. alba*, *M. rubra* and hybrid individuals from the herbarium specimens collected in between 1957-2006 (see Table 1 for sampling information). The leaf samples were ground to a fine powder using a mortar and pestle, and DNA was extracted using DNeasy Plant Mini Kit (Qiagen Corp., Valencia, CA). Polymerase Chain Reaction (PCR) amplification and sequencing of the chloroplast *trnL-trnF* and the nuclear ribosomal Internal Transcribed Spacer (ITS) DNA regions followed Piya and Nepal (2013).

RESULTS AND DISCUSSION

***Distribution of M. rubra at its northwestern boundary*—**Examination of *Morus* specimens housed in the regional herbaria allowed us to capture the taxonomic status of *M. rubra* and to determine its distribution at its northwestern boundary. We encountered several instances in which one species was confused

Table 1. Voucher information of* Morus *herbarium specimens used for developing DNA sequences. Each row contains taxon name, voucher information (abbreviations for herbaria follow Holmgren et al. 1990), and GenBank accession number.

Taxon	Voucher information (Herbarium)	Genbank accession number
M. rubra	RF Thorne-18414, Des Moines Co., Iowa, 1957 (ISC)	KF672603/ KF672605
M. alba	GE Larson-11296, Clay Co., South Dakota, 2008 (SDC)	KF672604
M. rubra x alba	SB Rolfsmeier-14341, Thurston Co., Nebraska, 1999 (NEB)	KF672606
M. alba x rubra	RF Thorne-3909, Monona Co. , Iowa, 1957 (ISC)	KF672607
M. alba x rubra	MM Garabrant-678, Washington Co. Nebraska, 1987 (NEB)	KF672608

with the other. Two examples of incorrect identification are presented in Figure 2 and 3.

After keying out the specimens using a suite of morphological characters (Nepal 2008) and annotating them, we confirmed the occurrence of *M. rubra* in Iowa, Kansas and Nebraska, but not in Minnesota and South Dakota (Table 2). We confirmed the occurrence of *M. rubra* in 24 counties of Iowa in contrast to only nine counties listed in the USDA PLANTS database (2012). We also found that earlier identification of the specimens from five of the nine counties was incorrect: *Morus* specimens from Cass, Hamilton, Harrison, Madison and Pottawattamie County were either *M. alba* or hybrid individuals. We did not find any herbarium record of *M. rubra* from South Dakota (SD), and our field exploration of the southeastern SD confirmed the absence of *M. rubra* from the state. We did not find *M. rubra* records from as many counties of Kansas where it had been reported earlier. We confirmed the oc-

***Figure 2.* Morus alba *specimen. The specimen was previously identified as* M. rubra.**

***Figure 3.* M. alba x rubra *specimen. The specimen was previously identified as* M. rubra.**

currence of *M. rubra* in 41 counties of Kansas as shown in Table 2. Previously identified specimens from other western and northwestern counties identified as *M. rubra* were *M. alba* or hybrid individuals.

We examined *M. rubra* specimens collected from Nebraska (NE) and confirmed the occurrence in Cass, Douglas, Gage, Johnson, Lancaster, Nemaha, Otoe, Pawnee, Richardson, Sarpy and Saunders Counties. We observed one healthy population of *M. rubra* in Indian Cave State Park (Richardson Co., NE). Previously, The Flora of Nebraska listed 19 counties for the occurrence of *M. rubr*a in Nebraska (Kaul et al. 2006): Cedar, Dixon, Dakota, Thurston, Washington, Dodge, Douglas, Saunders, Sarpy, Cass, Lancaster, Otoe, Nemaha, Johnson, Pawnee, Richardson, Gage, Jefferson and Webster. The USDA PLANTS distribution map has listed 11 counties (Table 2). One of us (MPN) annotated the herbarium specimens housed at NEB. The specimens collected from the northeastern counties such as Cedar, Knox, Dixon and Dakota were incorrectly identified; the majority of them were *M. alba* with a few specimens from hybrids (*M. alba* x *rubra*, introgressed with *M. alba* as the maternal parent).

In Minnesota, the only counties where the USDA PLANTS distribution map included *M. rubra* were Rice and Houston counties. We examined herbarium specimens of *Morus* from both counties and surveyed the areas from where the specimens were collected. As a result, we confirmed that those areas had only sporadic *M. alba* or hybrid trees. The documented occurrences of *M. rubra* in Minnesota were based on two herbarium records: one collected in 1899 and other in 1920. The former specimen (collection # 968 by H.L. Lyon, MINN) was collected from Jefferson (Houston Co. MN). The specimen offered very limited locality information. The latter specimen collected by Rosendahl and Butters (collection#3890, MINN) reports the locality as "sandy soil, wooded hillside about 3 miles north of Jefferson." We explored the area during the summer of 2010, and we were not able to locate any *M. rubra* trees. We communicated with Minnesota Department of Natural Resources (DNR) botanist, Welby Smith, who also claimed that *M. rubra* had not been found in either loca-

Table 2.* M. rubra *distribution at its northwestern boundary.

State	Counties (USDA 2012)	Counties (this study)
Iowa	Cass, Fremont, Hamilton, Harrison, Madison, Mills, Monona, Pottawattamie and Taylor	Benton, Cedar, Dallas, Davis, Decatur, Des Moines, Fremont, Henry, Johnson, Jackson, Jasper, Jones, Lee, Linn, Louisa, Mahaska, Marion, Mills, Monona, Muscatine, Page, Taylor, Warren and Washington
Kansas	Allen, Anderson, Atchison, Barber, Barton, Bourbon, Brown, Butler, Chase, Chautauqua, Cherokee, Clay, Cloud, Coffey, Cowley, Crawford, Decatur, Dickinson, Doniphan, Douglas, Elk, Ellsworth, Franklin, Geary, Greenwood, Harvey, Hodgeman, Jackson, Jefferson, Johnson, Labette, Leavenworth, Lincoln, Linn, Lyon, Marion, McPherson, Miami, Montgomery, Morris, Nemaha, Neosho, Norton, Osage, Osborne, Ottawa, Pottawatomie, Reno, Republic, Rice, Riley, Saline, Sedgwick, Shawnee, Summer, Trego, Wabaunsee, Washington, Wilson, Woodson and Wyandotte	Allen, Anderson, Atchison, Bourbon, Brown, Butler, Chase, Chautauqua, Cherokee, Clay, Coffey, Cowley, Dickinson, Doniphan, Douglas, Elk, Franklin, Geary, Greenwood, Harvey, Jackson, Johnson, Labette, Linn, Lyon, Marian, Marshall, McPherson, Miami, Montgomery, Morris, Nemaha, Osage, Pottawatomie, Riley, Saline, Sedgwick, Shawnee, Sumner, Wabaunsee and Woodson
Minnesota	Houston and Rice	None
Nebraska	Brown, Douglas, Furnas, Hall, Jefferson, Lancaster, Nemaha, Otoe, Richardson, Washington and Webster	Cass, Douglas, Gage, Johnson, Lancaster, Nemaha, Otoe, Pawnee, Richardson, Sarpy and Saunders
South Dakota	**	None

** Counties unspecified.

tion. In addition, we extended our exploration to various areas of the Richard J. Dorer (RJD) Memorial Hardwood Forest in southeastern Minnesota including two sites in Houston Co., where we explored the Reno and Oak ridge areas. We found sporadic *M. alba* and hybrid individuals (*M. alba* x *rubra*), but did not find any *M. rubra* trees in the area. There were three small to medium-sized hybrid trees in the vicinity of the documented sites. The presence of sporadic hybrid individuals in the RJD Memorial Hardwood Forest led us to explore the surrounding areas, particularly the east bank of Mississippi River in Wisconsin. We found one healthy *M. rubra* population in the core of the forest in Wyalusing State Park (Grant Co.) about three miles away from another population where both species occur in sympatry. Hybrid *Morus* individuals were abundant in the disturbed areas particularly along roadsides and around picnic areas. This locality seems like a promising site for assessing natural hybridization between the two species in future.

Is hybridization complicating Morus taxonomy?—Nuclear and chloroplast phylogenies of the genus *Morus* have indicated that *M. rubra* and *M. alba* are non-sister species (Nepal and Ferguson 2012). Despite their phylogenetic distance and geographic separation of over 20 million years, the two species undergo introgressive hybridization in the majority of habitats where they occur in sympatry (Burgess et al. 2005; Nepal 2008). Flowering time of the two species overlaps, and experimental hybridization between these species is successful in both directions (Burgess et al. 2005). Evidence from herbarium specimens reveals that hybridization in *Morus* is not a novel process, as was speculated over sixty years ago (see the herbarium record collection #Dunn12465, MINN; herbarium specimen identified as hybrid between *M. alba* and *M. rubra* in May 1, 1957). Hybridization and asymmetrical introgression were recently documented between these species in southern Ontario, Canada using RAPD markers (Burgess et al. 2005). They found that introgression towards *M. alba* as the maternal parent was higher than towards *M. rubra* as the maternal parent; the exotic species had a higher proportion of pollen production that resulted in seed discounting in the native species; as a result the native species was found to be less fit than both the hybrid and *M. alba* individuals.

Chloroplast *trnL-trnF* DNA sequences (= chlorotypes) from herbarium specimens of hybrid individuals are shown in Table 3. Each hybrid had one of the two types of chlorotypes. The two chlorotypes were species specific and differed by 6 bp indel (insertion/deletion). The chlorotype of the hybrid *M. alba* x *rubra* had "*M. alba* chlorotype" (with the 6 bp deletion), while *M. rubra* x *alba* had "*M. rubra* chlorotype" (with an 'the 6 bp insertion). The *trnL-trnF* gene region seems promising for assessing the direction of introgressive hybridization between the two species. The nuclear ITS DNA sequence variation between the two species is shown in Table 4. Occurrence of both species in sympatry in the majority of populations and overlapping flowering time of the species create an optimum environment for interspecific hybridization, which has been documented previously (Burgess et al. 2005; Nepal 2008). Consistent with their

Table 3. Screenshot showing chloroplast* trnL-trnF *sequence variation among* M. rubra*, hybrid and* M. alba *samples. In each row is the GenBank accession number for the sequence followed by taxon name, sample locality, and a section of* trnL-trnF *data matrix showing species specific differences at various character positions. Hybrid taxon contains "x" between species epithets; the first species in the combination refers to inferred maternal parent. DNA sequences for the samples with the collection year in parentheses were developed from the herbarium specimens and rest of the sequences were acquired from the GenBank.

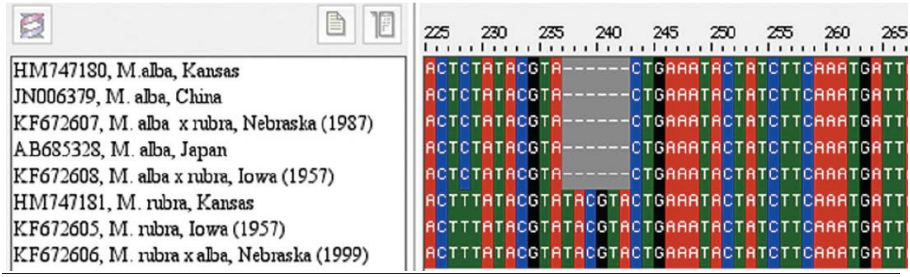

Table 4. Nuclear ITS sequence variation between* M. rubra *and* M. alba *samples. The table is modified from Nepal et al. (2012). Voucher information includes GenBank accession number, taxon name, sample locality, and base pair positions in the aligned data matrix for which there are differences among the sequences. Accessions in bold are the DNA sequences developed using samples obtained from herbarium specimens. The number in the parentheses represents the collection year.

Voucher information	18S ITS1 ITS2
	11223445555666
	26677777777778898801801166922 3
	76901234567890187898103503578 6
HM747165*, M. rubra, Kansas	GCCGTGCGCAATGCGCTTTGTTTTATACGT
HQ144176, M. rubra, Missouri	GCCGTGCGCAATGCGCTTTGTTTTATACGT
KF672603, M. rubra, Iowa (1957)	GCCGTGCGCAATGCGCTTTGTTTTATACGT
KF672604, M. alba, South Dakota (2008)	AT----------TCCCACCACGCGTTC
HM747164, M. alba, Kansas	AT----------TCCCACCACGCGTTC
AM041998, M. alba, India	AT----------TCCCACCACGCGTTC
AY345145, M. alba, China	AT----------TCCCACCACGCCTTC

findings, we also observed abundant hybrid individuals in the majority of sympatric populations. In our field observations, hybrids between the species were more common in the areas where both species co-occurred and the direction of introgression was biased towards the *M. alba* maternal parent. This further intensifies threats to the existence of the rare populations of the native *M. rubra* through genetic swamping (Burgess et al. 2005; Nepal 2008).

Taxonomic confusion in the two species of *Morus* is perhaps due to the highly varying magnitude and direction of inrogressive hybridization (Burgess *et al.* 2005) and morphological plasticity (Gray and Gray 1987). Morphologically, *M. rubra* is relatively less plastic than *M. alba* and hybrid individuals. In our field observation, we consistently encountered hybrid individuals in each sympatric population with various degrees of additive inheritance between the parental taxa.

Diagnostic features of *M. alba* and *M. rubra*—Morphological characters of the leaf, bud, branch and bark that distinguish *M. rubra* from *M. alba* are listed in Table 5. Using only leaf characters can be a challenge because young leaves of both species may look similar. *M. rubra* mature leaves are significantly larger than those of *M. alba*. In *M. rubra*, the upper leaf surface is rough and dull green, the lower leaf surface is densely hairy, the leaf base is often heart-shaped, and the leaf apex is acute, acuminate or subcaudate. Teeth on the leaf margin are regularly pointed. On the lower surface, the main vein color almost matches the color of the leaf. *M. alba* leaves are usually bright green, smooth and shiny on the upper surface with hairs concentrated along the main veins on the lower surface. A more rounded leaf base, obtuse leaf apex and the margin with rounded teeth are the distinguishing features of *M. alba*. On the lower surface, the main vein color contrasts more with the leaf surface than in *M. rubra* (see Nepal et al. 2012 for the type specimen image). The winter buds of *M. rubra* are larger than those of *M. alba*. The bud scale margins of *M. rubra* have a darker apical band, while those of *M. alba* have a white or lighter brown apical band. *M. rubra* has

***Table 5. Morphological features that distinguish the native* M. rubra *from its exotic congener* M. alba .**

Features	*M. rubra*	*M. alba*
Tree Size	Height up to 25m, diameter at breast height (DBH) small to large up to 1m.	Height up to 15m, DBH small to very large, up to 2-3m.
Habitat	Riparian areas, natural forested areas.	Open areas, common in disturbed areas, generic opportunist, can occur in both open and riparian areas.
Distribution	Northeastern America (from the Atlantic coast to the eastern edge of the Great Plains, north to S. Ontario Canada).	Cosmopolitan, native to China, naturalized, exotic invasive in North America.
Leaf	Leaf blade 5-40 x 3-28cm, base typically cordate, petiole 2-2.5cm. Leaf surface adaxially rough and dull green, abaxially densely pubescent (hairs all over but more along the veins), veins are more or less matching to the surface. Leaf apex acute, acuminate to subcaudate. Leaf margin regularly serrated (serrations pointed and acute).	Leaf blade 2-20 x 1.5-18cm, base usually truncate, petiole 2.5-5cm. Leaf surface adaxially smooth and lustrous, few hairs along the veins abaxially, veins are more prominent (distinct). Leaf apex obtuse. Leaf margin irregularly dentate (serrations often blunt or obtuse).
Winter bud	Larger (0.4-0.8cm) often with acute apex; the bud scale margins have a darker apical band.	Smaller (0.3-0.5cm) with often rounded apex, the bud scale margins have a lighter brown apical band.
Bark	Grayish bark with flattened, thinner ridges that peel back in older trees.	Reddish or tan bark with thick and solid ridges.
Branching pattern	Planar (flat) and spreads like less or more horizontal.	Diffused giving plants a rounded or bushy appearance.
Pistillate Flowers	Perianth greenish purple with white stigma branches.	Perianth greenish yellow with brown stigma branches.
Fruit	Cylindric, 1-4.5 x 0.5-1.5cm, deep purple to red.	Ovoid/ellipsoid, 1-3 x 0.5 -2cm, variable color from all white to pink to red.

Figure 4. Morphological character of the bark (A = Morus alba, B = hybrid individual and C = M. rubra).

grayish bark with flattened, thinner ridges that peel back in older trees (Figure 4). *M. alba* bark forms thick solid ridges that are more of a reddish tan coloration. The branching of a mature *M. rubra* is widely spaced, and the branches often grow horizontally giving the plant a planar appearance, while in *M. alba* the branching is more diffused giving the plant a bushy appearance. The two species differ in fruit shape and size: *M. rubra* has a long cylindric fruit, while *M. alba* has an ovoid or ellipsoid fruit. In addition to morphological characteristics, the two species differ in chloroplast *trnL-trnF* and nuclear ITS DNA sequences. These two gene regions seem promising markers for future projects on assessing the magnitude and direction of introgressive hybridization.

In summary, this project has clarified the geographic range of *M. rubra* at its northwestern boundary and provided insights into potential threats to *M. rubra* posed by the overly spreading exotic congener *M. alba* in the Midwest United States. We think addressing taxonomic misconceptions and clarifying the diagnostic features of the two species are critical steps towards developing management strategies for *M. rubra* in the United States.

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