REMNANT FOREST STANDS AT A PRAIRIE ECOTONE SITE: PRESETTLEMENT HISTORY AND COMPARISON WITH OTHER MAPLE-BASSWOOD STANDS

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Abstract: The maple-basswood community type has long been associated with the "Big Woods" of Minnesota and adjacent Wisconsin, although this community type also exists in discontinuous phases within surrounding forest types. This study looks at the apparent most northwestern outlier of the maple-basswood community type, Rydell National Wildlife Refuge (NWR) in Minnesota. Specific goals are (1) to determine if the maple-basswood stands at Rydell NWR existed historically, and (2) to compare the composition of the Rydell NWR stands to maple-basswood "core" sites, as well as other outlier sites. Public Land Survey records for the period between 1872 and 1876 for a 16-township block encompassing Rydell NWR indicate that, although this area was dominated by an oak-aspen forest type, a distinct maple-basswood region existed prior to European settlement and this had escaped disturbance from fire and wind. Present-day stand composition data from six Rydell stands are compared with published data from other maple-basswood stands, using detrended correspondence analysis. A strong geographic pattern is indicated in the ordination diagram, which is attributed to differences in September precipitation and actual evapotranspiration between the sites. Local-scale environmental gradients act to modify the dominant climatic trend on composition, however, as some Rydell stands plotted closely to the core region in ordination space, whereas other Rydell stands demonstrated greater similarity to oak and aspen stands in North Dakota. [Key words: forest-prairie ecotone, maple-basswood, presettlement vegetation, ordination, Minnesota.]

INTRODUCTION

The maple-basswood community occupies the smallest geographic extent of the deciduous forest types of eastern North America (Braun, 1950). The largest continuous area of maple-basswood occurred in the "Big Woods" region of south-central Minnesota, adjacent southwestern Wisconsin, and extreme northwestern Illinois (Fig. 1). Daubenmire (1936) conducted an extensive study of the Big Woods region, and popularized the notion that this area was dominated by sugar maple *(Acer saccharum)* and American basswood *(Tilia americana),* although it is evident that other species, notably elm (*Ulmus* spp.), were also dominant in this region. Compositional variations are evidenced throughout the range of the maple-basswood community

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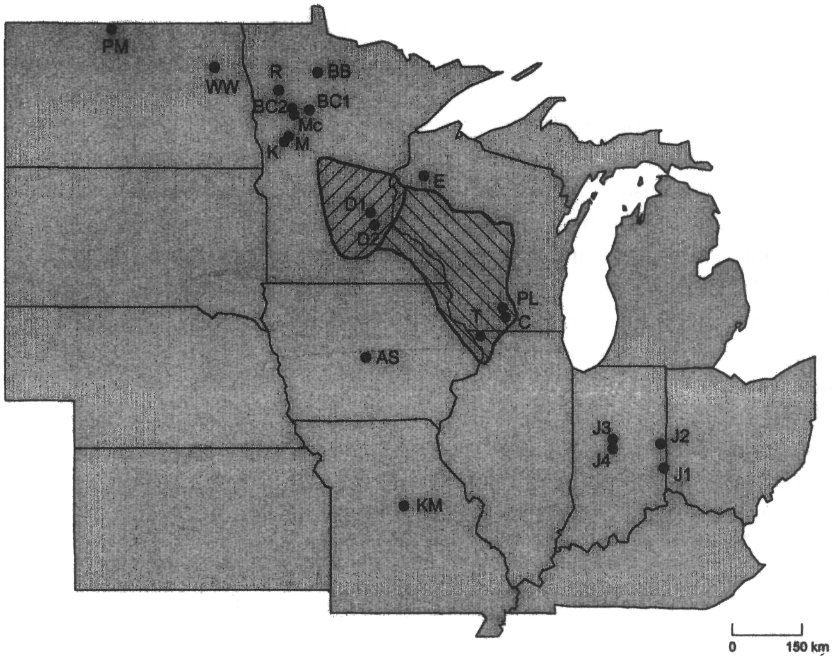

Fig. 1. Location of studies included in the analysis. Rydell NWR is indicated by "R." See Table 1 for an explanation of other site codes. The maple-basswood "core" is indicated by cross-hatching, and includes the "Big Woods" section in southern Minnesota and the adjacent Driftless section to the southeast (Braun, 1950).

type. For instance, beech *(Fagus grandifolia)* begins to replace basswood as the codominant with maple towards the community's southeastern limits, and other species such as hickory (*Carya* spp.), black walnut *(Juglans nigra)*, butternut *(Juglans cinerea)*, and black cherry *(Prunus serotina)* take on increasing prominence; approaching the northern limits, sugar maple may become less dominant, and elements of the northern pine forests such as balsam fir *(Abies balsamea)* enter the community. In other areas, oak (especially northern red oak *[Quercus rubra]* and bur oak *[Q. macrocarpa]*), yellow birch *(Betula alleghaniensis)*, paper birch *(B. papyrifera)*, ash (*Fraxinus* spp.), and elms co-occur with maple and basswood (Heinselman, 1974).

An extensive literature exists on the environmental factors responsible for the distinctiveness of the maple-basswood forest type; most cited are the interdependent influences of climate, fire, and edaphic/geomorphic setting. The cessation of recurrent fire is widely believed to account for the rapid, synchronous expansion of the maple-basswood community type in the late Holocene (Grimm, 1983). In the absence of fire, prairie succeeds to oak savanna, then to oak woodland, and eventually to the "climax" maple-basswood community type (Lindsey and Escobar, 1976). The occurrence of maple-basswood in sheltered "pockets" within the northern conifer forest and prairie vegetation types, and the importance of surface water patterns and topographic breaks delineating the boundaries of maple-basswood from other community types, supports the view that fire is critical in limiting the extent of maple-basswood (Daubenmire, 1936; Harper, 1963; Grimm, 1984). Grimm (1983) suggests that bigwoods vegetation (dominated by elm, basswood, ironwood *[Ostrya virginiana]*, and sugar maple) is a recent (<400 years) community type, attributable to the onset of cooler, wetter climatic conditions that reduced the fire frequency in the upper Midwest. Grimm's work suggests that a climate change was critical for the historical establishment of the maple-basswood community type through its influence on fire patterns, although others have suggested a direct link between climate change and the establishment of this community type (Buell and Cantlon, 1951). Additional research suggests that climate also is responsible for segregating the maple-basswood community type from other mesic forest types. Lindsey and Escobar (1976) plotted sites from Braun's (1950) forest regions versus climatic variables; the resulting figure depicts the maple-basswood region as having very limited climatic amplitude. With the exception of the hemlock-hardwood sites, representative sites of the maple-basswood community occur in the coolest and driest locations, with the lowest effective moisture of all forest regions.

Geomorphic setting or soils may play a contributing role in the distribution of maple-basswood because, with few exceptions, the community type tends to occur on glacial moraines, loam/silt loam soils, or on other fine-textured soils (Daubenmire, 1936; Buell and Cantlon, 1951; Buell and Bormann, 1955; Harper, 1963). To some extent, these more mesic settings afford protection against fire, but basswood especially seems to be sensitive to differences in microclimate caused by the soil-moisture regime and topography (Lindsey and Escobar, 1976; Crow, 1990). Soils and geomorphic setting therefore may reinforce *regional* patterns through their effect on fire occurrence, and they also may have *local-scale* effects regarding presence at a particular site.

Since the maple-basswood community type is linked so strongly with the Big Woods of southern Minnesota and adjacent Wisconsin (the maple-basswood "core"), the actual geographic extent of communities in which maple and basswood dominate may not be fully recognized. Furthermore, although a literature exists regarding the separation of maple-basswood from other forest types, very few studies have examined variation *within* the maple-basswood forest type. One of the goals of the present study will be to compare compositional variation between Rydell National Wildlife Refuge (NWR), an outlier site of the maple-basswood community type in western Minnesota, with stands of the "core" and with other maple-basswood sites from throughout the range of this community type.

Fieldwork was conducted at Rydell NWR in 1994 to provide baseline compositional data on the remnant stands and to document the effects of a catastrophic windstorm that occurred on June 19, 1994 (Dyer and Baird, 1997). A noteworthy finding of the study was the compositional diversity of the different forested stands located in such close proximity within the Refuge, including the apparent most northwestern extent of the maple-basswood community type in North America.

The goals of the present study are (1) to examine the Public Land Survey records for the region encompassing Rydell NWR to see if these maple-basswood stands, which characteristically occur on protected sites where catastrophic fires were historically rare, were evident before European settlement (and the suppression of fire); and (2) to compare the composition of the ecotonal Rydell stands with published data for other maple-basswood sites, using ordination. The intention is to ascertain whether compositional differences exist between stands situated at an ecotone and those at core locations, whether these differences might have existed historically, and, finally, whether regional environmental gradients are expressed through compositional differences among geographically diverse stands within the maple-basswood community type.

STUDY SITE

Rydell NWR was established in 1992 in northwestern Minnesota, situated on 859 ha adjacent to Maple Lake in Polk County. The Refuge, located at the prairie-forest boundary, contains a patchwork of wetlands, old fields, conifer plantations, a bog, and remnant stands of mesic deciduous forest, including stands of maple-basswood. A previous study reported results of vegetation sampling conducted on six stands within the Refuge (Dyer and Baird, 1997). Although these stands (ranging in size from 6 to 20 ha) are all within 2 km of each other, they exhibit very different compositions. Three maple-basswood stands are dominated by sugar maple, basswood, and ironwood in the canopy. Ten of the 33 woody species in these three maple-basswood stands represent the northern and/or western-most extent of that particular species in Minnesota (Ownbey and Morely, 1991). Dominant canopy species also dominate the understory, along with the deciduous shrub leatherwood *(Dirca palustris)*. The herbaceous flora reflects a transitional nature of this community type, with northern species (including wild sarsaparilla *[Aralia nudicaulis]*, Canada mayflower *[Maianthemum canadense]*, and nodding trillium *[Trillium cernuum]*), occurring with more southern species (such as rattlesnake fern *[Botrychium virginianum]*, bellwort *[Uvularia grandiflora]*, bloodroot *[Sanguinaria canadensis]*, and blue cohosh *[Caulophyllum thalictroides]*). In contrast to the maple-basswood stands, the three other surveyed stands are dominated by aspen *(Populus tremuloides)* and oak, especially bur oak, characteristically considered "prairie invader" species along the ecotone. Native vegetation associated with the dominant soils at Rydell NWR is either prairie, or mixed hardwoods and prairie (USDA NRCS, 1995, 1997), indicating the potential of a past history of woodland invasion of existing grassland at these ecotonal sites. Field observation and comparison with soil surveys indicate that compositional differences among the six surveyed stands can be attributed largely to surface runoff and drainage conditions, with the maple-basswood stands occurring on the better-drained sites. According to a long-time resident whose family was among the original settlers, present-day stands on the Refuge had never been clearcut since European settlement of the area in the 1880s; selective cutting (especially for aspen) is known to have occurred, however, and one stand also was used as a "sugarbush" for maple syrup production. Fires have been suppressed by residents of the area, and typically did not affect the overstory directly. Except for "emergency" grazing, particularly during the dry years of the 1930s, grazing by cattle historically has been minimized by fencing; severe overgrazing by white-tail deer, however, is now quite evident on the Refuge.

Braun's (1950) map of eastern deciduous forest regions places Rydell NWR in a thin Oak-Hickory Forest Region separating the Grassland/Prairie Formation in the west from the Hemlock-White Pine-Northern Hardwoods Region to the east. She acknowledges, however, that the maple-basswood type is difficult to delineate, since it is represented over a broader geographic area, as discontinuous areas within other forest types (these limitations would hold true for any vegetation map produced at such a small scale). The Rydell site falls along the periphery of Omernik's (1986) North Central Hardwood Forest Ecoregion, adjacent to prairie; potential natural vegetation is characterized by maple and basswood, along with northern hardwoods. Bailey (1995) places this area within the extensive Eastern Broadleaf Forest (Continental) Province, at the boundary with the Prairie Parkland (Temperate) Province. He characterizes this ecoregion as dominated by oak and hickory, with increasing numbers of maple and basswood occurring in the northern reaches.

Maps by Upham (1895) and Marschner (1974) depict vegetation for this region near the time of European settlement. Upham provided a detailed map of forested areas based on field observations along the southern portion of the former glacial Lake Agassiz. His map (at an approximate scale of 1:2,700,000) clearly places the area to the east of Maple Lake (the location of the Rydell NWR) right on the prairie-forest boundary. Marschner's map of Minnesota, based largely on survey notes, maps, and descriptions of the original land survey, depicts the general area around the Rydell NWR as a wooded "peninsula" of aspen parkland surrounded by upland prairie. A closer examination of a 16-township area on Marschner's map shows this area centred on the Refuge to be a mosaic of prairie, brush prairie, aspen-oak land, and "Oak Openings and Barrens," an area of which is centered on the Refuge itself. Interestingly, a generalized map from Marschner presented in McAndrews (1966) shows the area around the Refuge as a small island of maple-basswood forest, within another small island of oak-aspen forest surrounded by prairie.

DATA AND METHODS

Public Land Survey Records

To determine community composition before European settlement and explore what environmental factors may be responsible for the presence of the Refuge's maple-basswood stands, copies of the original surveyor notes, maps, and descriptions were obtained from courthouse records for the 16-township area situated over the wooded "peninsula" indicated on Marschner's map; Rydell NWR is located near-center of this 4-by-4 township grid (T146N R41W-T149N R44W). These townships were surveyed by the General Land Office between 1872 and 1876. Bourdo (1956) and Almendinger (1996) provide details for using survey records for reconstructing past vegetation, including potential biases (e.g., species or size-class preferences) on the part of the surveyors in the selection of bearing trees. The present study only examines location of trees for descriptive purposes and does not attempt a quantitative analysis of species composition; the effects of these biases therefore should be minimized.

The species, size, and location were transcribed from survey notes for each bearing tree at quarter-section and section corners (i.e., at 0.8-km [half-mile] and 1.6-km

[1 mile] grid intersections). In addition, this information also was transcribed for "meander corners" (which marked section line locations away from corners, for instance where they intersected lakes) for the township containing the Refuge and the adjacent township to the east (T148N R 42-43W). In addition to marking bearing trees to delineate township lines, surveyors also were instructed to record information regarding cover type along the section lines (brush prairie, hardwood timber, aspen, etc.), and to note areas in windfall, or timber areas that had been burned. This information also was transcribed from the Public Land Survey records.

Comparison with Other Maple-Basswood Stands

A second goal of this investigation is to compare characteristics of the ecotonal Rydell stands with other maple-basswood stands. To this end, published studies were collected that included community data for sites described as "maple-basswood," or that clearly fit this distinction. Starting points for the search included Braun's (1950) description of the maple-basswood region, Curtis's (1959) description of the maple-basswood region of Wisconsin, Heinselman's (1974) discussion of the vegetation of Minnesota, and Daubenmire's (1936) study on the Big Woods area of Minnesota. Since European settlement, the area characterized by the maple-basswood community type has been greatly modified by human activity, especially clearing for agriculture. As early as the 1930s, researchers appreciated the great reduction in the extent of this community type. Indeed, the impetus for the collection of data referenced in this study often was to document the community type while remnant stands still existed. Although some of these remnant stands are rather small, all the selected maple-basswood sites were characterized by the original authors as "virgin," "near-virgin," "old-growth," or at least "relatively undisturbed." Included in the selected maple-basswood sites was one site (BCI; see Fig. 1; also see Table 1 for abbreviations) in the "tension zone" with the conifereous forest region (containing balsam fir, white spruce *[Picea glauca]*, and eastern white pine *[Pinus strobus])*, and four sites (J1-J4) transitional to the beech-maple forest type. In addition to these maple-basswood sites, data from two hardwood stands in North Dakota (PM and WW), disjunct from the Rydell stands and separated by intervening prairie, also were included for comparative purposes. One of these sites (WW) was not characterized as undisturbed.

Vegetation sampling methods obviously varied among the studies that were deemed potential candidates for inclusion in the present analysis; since the data presented in these studies were in varied formats, a standardization was necessary for comparative purposes. The greatest number of studies could be included if density values (relativized, either as published or calculated for this analysis) were used. Sixteen studies, representing compositional data on 50 arboreal species in 42 stands, were used in the analysis. Table 1 lists data sources for this analysis, and Figure 1 depicts their locations. Most sites occur away from the maple-basswood core. To allow the most direct comparison with the Rydell data, when possible 10 cm (4 inches) was the minimum DBH size-class extracted from the published data. For seven studies this was not possible, and a different minimum DBH size-class was used (K, M, PM: 2.5 cm; J, P: 7.6 cm; T: 15.2 cm; WW: 25 cm). One study (Mc) collected

Table 1. Sources of Compositional Data for Ordination, Study Locations, and Site Abbreviations

Abbreviation	Data source
AS	Aikman and Smelser (1938) Story and Boone Counties, Iowa *Maple-Linden Community* (AS1), *Transition Community* (AS2)
BB	Buell and Bormann (1955) Beltrami County, Minnesota *Sugar Maple-Basswood Stand*
BC	Buell and Cantlon (1951) Mahnomen County, Minnesota *Itasca Stand* (BC1), *Waubun Stand* (BC2)
C	Curtis (1959) Green County, Wisconsin *"Typical Southern Mesic Forest Stand"*
D	Daubenmire (1936) Hennepin and Rice Counties, Minnesota *Minnetonka Woods* (D1), *Northfield Woods* (D2)
E	Eggler (1938) Washburn County, Minnesota *Hunt Hill* (E1), *Long Lake Woods* (E2), *East Woods* (E3)
J	Jones (1951) Union, Randolph, Clinton, and Boone Counties, Indiana *Union/Stand A* (J1), *Lynn/Stand B* (J2), *Smith/Stand L* (J3), *Randel/Stand M* (J4)
K	Kiehne (1980) Otter Tail County, Minnesota *Maplewood State Park, Stands 1-10* (K1-K10)
KM	Kucera and McDermott (1955) Boone County, Missouri *Douglas Woods* (KM1), *Schnabel Woods* (KM2)
M	Medhaug (1985) Otter Tail County, Minnesota *Maplewood State Park, Adjacent Lands* (Average of 8 Stands)
Mc	McAndrews (1966), Becker County, Minnesota *Reichow Stand*
PL	Peet and Loucks (1977) Dane and Green Counties, Wisconsin *Stands 02* (PL1), *03* (PL2), *91* (PL3), *93* (PL4)
PM	Potter and Moir (1961) Bottineau County, North Dakota *Scully's Woods, Unburned*
R	Rydell National Wildlife Refuge; Dyer and Baird (1997) Polk County, Minnesota *Oak Stand* (R1), *Maple-Basswood Stand 2* (R2), *Aspen Stand* (R3), *Maple-Basswood Stand 2* (R4), *Lowland Hardwood Stand* (R5), *Maple-Basswood Stand 1* (R6)
T	Telford (1926) Jo Daviess County, Illinois *"Average Acre"* (Measurements from all trees on 17.4 acres)
WW	Wikum and Wali (1974) Grand Forks County, North Dakota *Gallery Forest, Forest River Biology Area* (Average of 40 Stands)

data on "canopy trees," without reference to size classes included. Detrended correspondence analysis (DCA), an eigenanalysis ordination technique based on reciprocal averaging, was used to facilitate stand comparison (Gauch, 1982).

RESULTS

Public Land Survey Records

A tally of bearing trees for the entire study area clearly indicates that this site was primarily an aspen-oak woodland surrounded by prairie. The trees recorded in descending order of occurrence are: aspen (n = 992), oak (411), balm of Gilead (balsam poplar, *Populus balsamifera)* (83), elm (35), willow (*Salix* spp.) (26), paper birch (24), ash (19), lynn (American basswood) (13), ironwood (12), sugar maple (8),

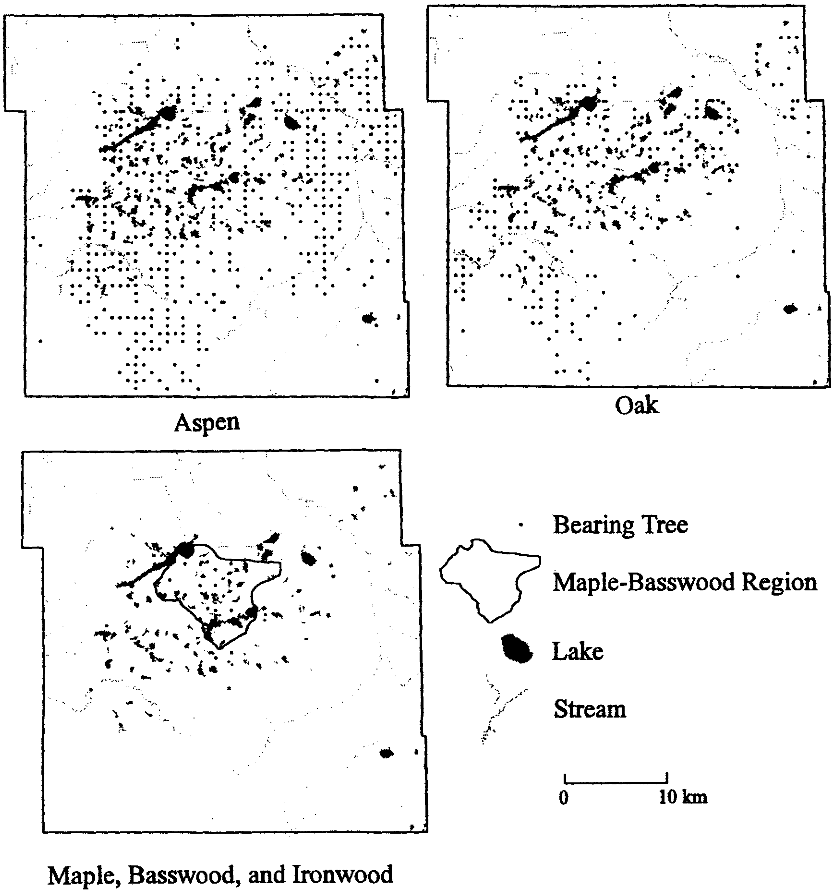

Fig. 2. Location of aspen, oak, and maple-basswood-ironwood bearing trees at quartersection and section corners for a 16-township area centered on Rydell NWR. See Figure 1 for location of this area. Maple Lake is situated along the northwest boundary of the Maple-Basswood Region.

and tamarack *(Larix laricina)* (7). Figure 2 depicts the occurrence of corner- and quarter-section bearing trees of aspen, oak (predominantly bur oak), and a maple-basswood-ironwood composite. Comparing the location of trees versus prairie at the time of the survey with a map of geomorphic regions (physiographic areas defined by topographic relief and soil parent material) indicates an affinity of the bearing trees for loamy sites of the Fosston Till Plain and the Erskine Moraine (as opposed to the Mahnomen and Agassiz Inter-Beach Area Lacustrine Plains that also occur in the study area) (LMIC, 1989). When the locations of maple, basswood, and ironwood are considered in conjunction with surveyors' references to section lines dominated by "hardwood" (as opposed to "aspen" or "oak" timber), or when specific mention of the prevalence of maple or basswood along certain section lines was made, a "maple-basswood region" emerges (see Fig. 2). This maple-basswood region contains all but five of the maple, basswood, or ironwood bearing trees for the 16-town-

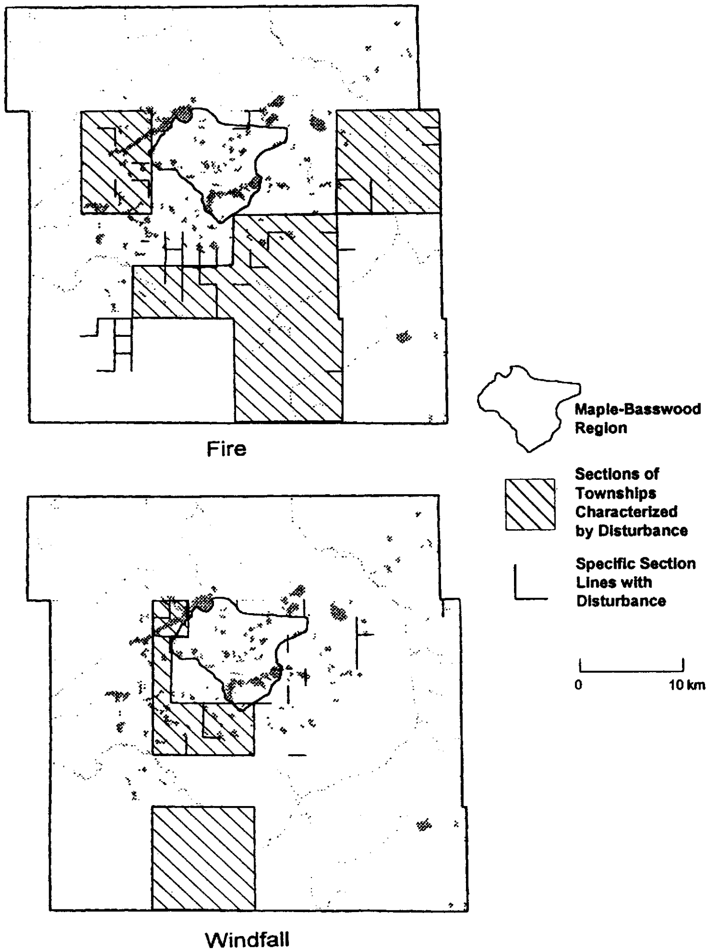

Fig. 3. Maple-basswood region in relation to specific section lines and sections characterized by fire or windfall in Public Land Survey notes.

ship study area, as well as virtually all of the section lines containing references to these species, or to "hardwood" timber. Just under half of the section lines within the delineated maple-basswood region are characterized with these specific cover types.

References to fire or windfall along specific section lines are depicted in Figure 3. In addition, sections where more general comments were made by the surveyors also are noted (e.g., "From all indications the whole township has at one time been covered with timber which had been destroyed by fire." "In the west portions there is much burnt land and aspen and willow brush. A great deal of timber is in windfalls—half blown down and the rest standing."). These disturbed areas are shown in reference to the maple-basswood region defined previously. This area had escaped disturbance by wind and fire at the time of the Public Land Survey.

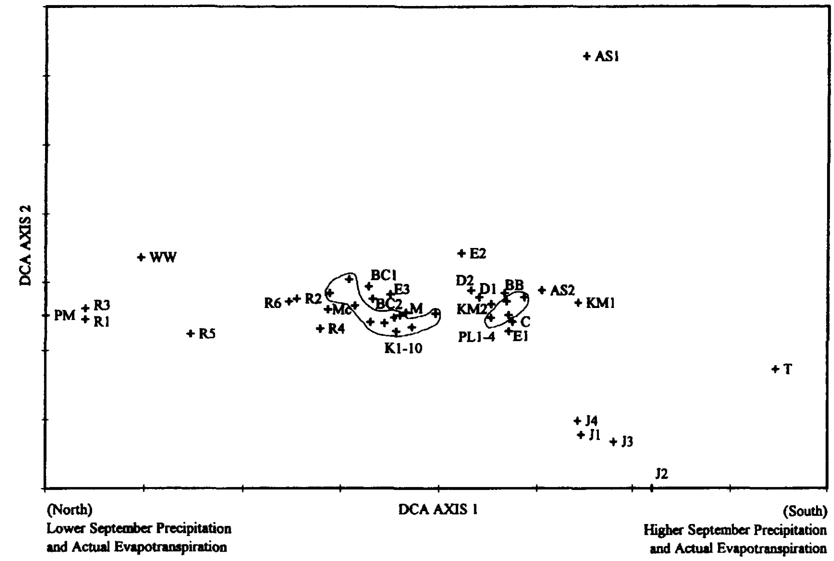

Fig. 4. Forty-two stands from the 16 studies of Figure 1 plotted against the first two DCA axes. See Table 1 for site abbreviations. The first axis reflects a latitudinal gradient of September precipitation and actual evapotranspiration. Sites to the left in the diagram contain greater proportions of bur oak, trembling aspen, green ash, and paper birch; sites to the right contain increased proportions of northern red oak, hickory, and walnut. The central portion of the axis represents the maple-basswood "core," and representative sites have higher densities of sugar maple, basswood, and ironwood. Sites K1 through K10 and sites PL1 through PL4 clustered near each other and for clarity are circled in the diagram. Axis 1: gradient length = 3.7, eigenvalue = 0.50; Axis 2: gradient length = 3.1; eigenvalue = 0.27. Rare species (<20% of maximum frequency) were downweighted in proportion to their frequency.

Comparison with Other Maple-Basswood Stands

A strong geographic pattern is apparent on the ordination diagram (Fig. 4), with the maple-basswood core (D1, D2, C, PL1-PL4 from Fig. 1) plotting out in the center of first axis, with a second cluster of points comprised of northern Minnesota sites, including three of the Rydell sites (R2, R4, R6). The core cluster also contains sites from Missouri (KM2) and the most northern Minnesota site (BB) that occurs on a sheltered location between Upper and Lower Red Lake. The northern Wisconsin sites (E1-E3) extend across both main clusters. Sites north of the core area have lower values on the first DCA axis, and those sites to the south (AS1, AS2, KM1, and J1-J4), have higher values ($r = -.78$ between stand latitude and Axis 1 scores). Westernmost sites (the North Dakota sites: PM and WW, and three Rydell sites: R1, R3, R5) form a cluster of sites with the lowest scores on Axis 1. This geographic pattern does not reflect a species richness gradient between the sites, but rather a waxing and waning of dominant species. Those sites to the left in the ordination diagram contain greater proportions of bur oak, aspen, green ash *(Fraxinus pennsylvanica),* and paper birch, whereas sites to the right in the diagram have increased proportions of northern red oak, hickory, and walnut. The stands clustering around the maple-basswood core and the adjacent cluster of northern Minnesota sites (including three Rydell stands: R2, R4, R6) have higher densities of sugar maple, basswood, and ironwood compared to the other sites. The Illinois site (T), which is within the maple-basswood core region in Figure 1, falls as an outlier with the highest score on Axis 1. This site shares some compositional similarities with the other core sites of neighboring southern Wisconsin, but stands alone because of its unique dominance by white oak *(Quercus alba)* and jack oak *(Quercus ellipsoidalis)*.

Axis 2 largely separates the Indiana sites (J1-J4), which have the lowest scores on Axis 2, and an Iowa site (AS1) that has the highest score on Axis 2. The Indiana sites are transitional to the beech-maple forest region, and contain several species not encountered in any of the other study sites (e.g., tulip poplar *[Liriodendron tulipfera]*, Ohio buckeye *[Aesculus glabra]*, American beech, black tupelo *[Nyssa sylvatica]*, swamp white oak *[Quercus bicolor]*, pin oak *[Q. palustris]*, and black oak *[Q. velutina]*). Although the Iowa site is dominated by maple and basswood, the maple species is black maple *(Acer nigra)*, causing this site to segregate from other sites in ordination space. The second Iowa site (A2) also contain black maple, but is more similar to the other maple-basswood sites in ordination space. It is described as a "transitional" community, and shows a greater proportion of oak, hickory, and elm.

The strong geographic pattern that emerges from the ordination diagram suggests a climatic control on community composition for these sites. To explore this possible link, each site was assigned to its nearest climate station (Willmott and Rowe, 1993). Actual distances between climate stations and study sites ranged from 4 to 40 km, with an average distance of 25 km. The relatively close proximity of climate stations to study sites suggests that the raw climate station values would reasonably describe long-term conditions at the study sites. Average monthly and annual temperature, precipitation, and actual evapotranspiration values for each site were correlated with that site's DCA Axis 1 score. The strongest correlations were with September precipitation and actual evapotranspiration (r = .88 and .86, respectively, $P \leq .0001$); in other words, southern sites had higher average September precipitation and actual evapotranspiration values compared to the northern sites.

DISCUSSION AND CONCLUSIONS

A maple-basswood region, as evidenced by the presence of the late-successional stands within the Rydell NWR, apparently existed before European settlement as an "island" within an aspen-oak "peninsula" extending into the western prairie. The maple-basswood region that emerges from an examination of Public Land Survey records occurs to the lee of the large (ca. 670 ha) Maple Lake, on a glacial till plain. Although aspen and oak also were located in this area, it is clearly not the "Oak Openings and Barrens" (consisting of oak groves or single trees in a matrix of xeric tall-grass prairie) as Marschner's popular map portrays. The importance of the geomorphic setting supports the observations of Buell and Cantlon (1951) that the western limit of the deciduous forest corresponds to the eastern margin of glacial Lake Agassiz. The sheltered nature of the Rydell location, along with the irregular topography and the resulting abundance of ponds and small lakes, would afford shelter from frequent prairie fires (Grimm, 1984), and this protected status presumably enabled the hardwoods to become established. In the 125 years since the Public Land Survey was conducted, and in the absence of fire, stands in this maple-basswood region located on the Rydell NWR have become increasingly dominated by maple, ironwood, and basswood. Continued fire suppression, and the fact that extensive agricultural land use acts as effective fire breaks, may be expected to continue this trend of dominance by maple-basswood at the expense of the oak-aspen communities.

At the time of the Public Land Survey, the maple-basswood region also appears to have escaped disturbance by wind that was fairly widespread in the oak-aspen areas elsewhere within the study area. This historic finding supports present-day observation (Dyer and Baird, 1997); the catastrophic windstorm that struck the Refuge in 1994 had minimal effects on the maple-basswood stands, but caused extensive damage in the early successional (aspen-dominated) stands. It was hypothesized that differential response could accelerate succession on the Refuge, resulting in greater maple-basswood dominance in the absence of other overriding controlling factors such as surface drainage and runoff.

Ordination of the Rydell stands, along with other maple-basswood stands, uncovered a strong geographic pattern that can be attributed to climatic patterns. Specifically, the emergence of September precipitation and actual evapotranspiration as explanatory variables suggest that drought stress and recharge are critical in explaining compositional variation among the study sites. The fact that temperature variables did not emerge as explanatory variables suggests that the key factors responsible for compositional variation within the community type are not the timing of the onset of the growing season or its length. Instead, drought stress at the end of the growing season seems critical. This may be a direct climatic effect, with component species demonstrating different sensitivities to drought stress. These differential sensitivities would be expected to be especially pronounced at the periphery of the community type, where species at the edges of their ranges would be susceptible to extreme climatic events that are more likely at these ecotonal sites. The emergence of drought stress as an explanatory variable also may indicate an indirect climatic effect through its influence on fire patterns. Increased fall precipitation reduces the annual probability of fire (Grimm, 1983).

Ordination results also suggest that the forested stands of Rydell NWR exhibit truly ecotonal properties. Three stands are much more characteristic of the more xeric forest stands found in North Dakota to the west, whereas the other three stands exhibit closer similarity to the maple-basswood core. Although a broad geographic gradient in community composition is evident from the ordination results, it is clear that local-scale environmental gradients are superimposed, modifying the climatic pattern. Compositional differences between stands within Rydell NWR are attributable to drainage differences, and possibly stand disturbance histories. The result is that these stands, situated within 2 km of one another, show stronger similarities to sites over 100 km distant, than they do to each other.

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