The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 154 October 2005 No. 2

Am. Midl. Nat. 154:273–285

Relationships Between Soil Characteristics, Distribution and Restoration Potential of The Federal Threatened Eastern Prairie Fringed Orchid, Platanthera leucophaea (Nutt.) Lindl.

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ABSTRACT.—The Federal threatened eastern prairie fringed orchid (*Platanthera leucophaea*) occupies prairies, sedge meadows, bogs and fens, primarily north of the Wisconsinan glacial boundary. In the Midwest, where restoration is a recovery objective, its southern distribution is thought to be limited by the transition from nutrient-rich Wisconsinan-aged soils to more acidic nutrient poor soils of Illinoian-aged glacial drift. To better understand edaphic factors affecting its distribution and potential for establishment of new populations, we analyzed soil characteristics across the range of habitats occupied by this species, as well as from unoccupied habitats on the Illinoian Till Plain. We found that *P. leucophaea* occupies a complex edaphic gradient in variation of % organic matter, base content and soil texture. On Wisconsinan-aged substrates, it occurs in circum-neutral base-rich organic prairie soils in Illinois and Wisconsin and in less calcareous soils with slightly higher pH and lower organic matter content in Michigan lake plain prairies. Eastern sand prairie and sedge meadow habitats on Wisconsinan-aged drift and on unglaciated soils are moderately acid and nutrient poor, while bog and fen habitats are more strongly acidic and highly organic, with no evidence for an underlying calcareous substrate. In comparison, unoccupied prairie soils on the Illinoian till plain have lower pH, % organic matter and base concentrations. These soils also have relatively high % silt content which results in comparatively low available soil moisture holding capacity. This combination of soil conditions may exceed the tolerance limits of *P. leucophaea* and prevent this species from occurring south of the Wisconsin glacial boundary in the Midwest. On the other extreme, calcareous fens have high pH levels as well as extremely high calcium concentrations, which may exceed the tolerance limits of this species. These findings have implications for guiding efforts to establish *P. leucophaea* into habitats that should be suitable for this species.

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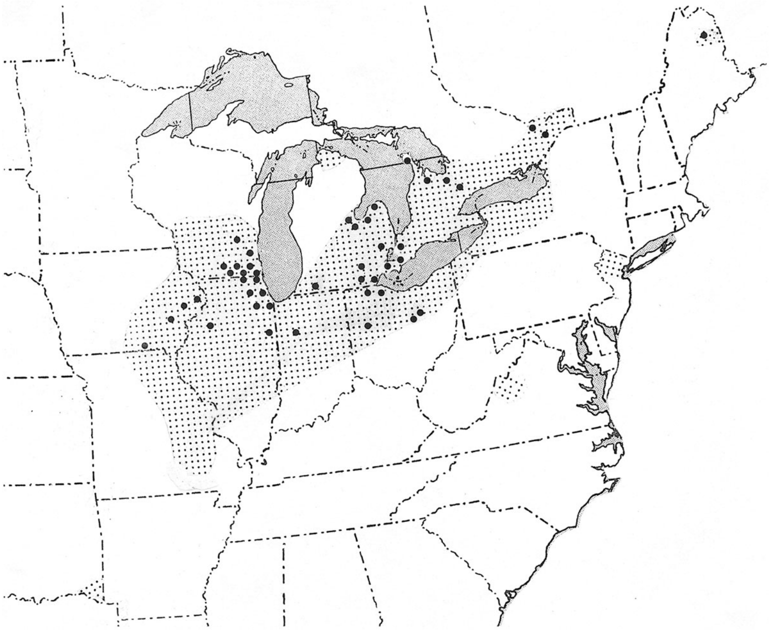

FIG. 1.—Former range (shaded) and current distribution (• = presumed extant county record) of *Platanthera leucophaea* in North America. Modified from Bowles (1983)

INTRODUCTION

Soil chemical and physical factors, especially pH, base concentrations and available moisture holding capacity, have strong effects on plant survival (Larcher, 1975). These factors vary in response to regional differences in soil parent materials and vegetation, which can play important roles in the establishment and distribution of orchid species (Wherry, 1918; Stuckey, 1967). Edaphic and habitat conditions, as well as presence of compatible mycorrhizal fungi, have been thought to control the distribution of the eastern prairie fringed orchid [*Platanthera leucophaea* (Nutt.) Lindl.] (Sheviak, 1974). This species formerly ranged across the prairie peninsula from eastern Iowa and Missouri through Illinois, Indiana and Michigan to Ohio, Pennsylvania, Ontario and New York, with disjunct populations in Maine, New Jersey and Virginia (Fig. 1). Remnant populations of *P. leucophaea* occur in midwestern prairies and prairie wetlands, in fens and sphagnum bogs in the eastern part of its range and in graminoid wetlands in outlying habitats in Ohio, Ontario, Missouri and Virginia (Bowles, 1983). In Illinois, the southern boundary of its distribution (Fig. 2) coincides with the edaphic transition from Wisconsinan-aged base-rich soils to more acidic nutrient-poor soils of the older Illinoian till plain, which also supported tallgrass prairie (Sheviak, 1974). This orchid ranges beyond the Wisconsinan glacial boundary in western and southwestern Illinois, apparently due to greater depth of Wisconsinan-aged calcareous loess along the Illinois and Mississippi River valleys (Fig. 2). Similar conditions, as well as habitat availability, probably affected the distribution of *P. leucophaea* eastward in Indiana and Ohio, where tallgrass prairie also tended to occur north of the Wisconsinan glacial boundary (Stuckey, 1981). Vertical stratification of pH may affect the micro-topographic distribution of different orchid species in bogs (Wherry, 1918). In accordance, where occurrences of *P. leucophaea* in acidic or nutrient poor habitats such as

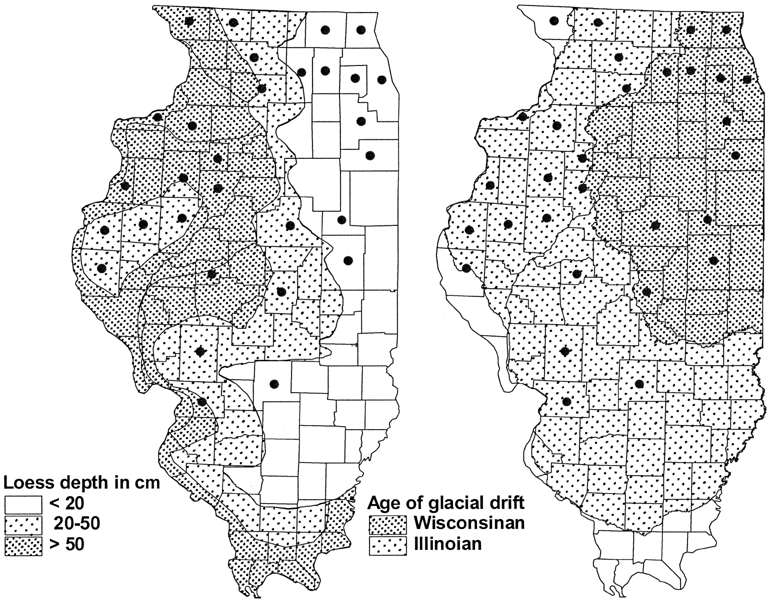

FIG. 2.—Former Illinois distribution (• = county records) of *Platanthera leucophaea* in relation to loess depth and age of glacial drift. Maps modified from Sheviak (1974), Fehrenbacher *et al.* (1984) and Piskin & Bergstrom (1967)

sphagnum bogs appear contrary to an acceptance of alkaline control of its habitat, they have been attributed to presence of underlying calcareous substrate or minerotrophic groundwater (*e.g.,* Correll, 1950; Steyermark, 1963; Sheviak, 1974; Case, 1987; Homoya, 1993). Some orchids are also thought to display bimodal distributions with respect to pH and nutrient concentrations (Sheviak, 1974; Niemann, 1975; Sheviak, 1983; Case, 1987), which could also affect the distribution of *P. leucophaea.* Curtis (1936) suggested that different species of mycorrhizal fungi associate with *P. leucophaea* across this range of habitats. However, these species are no longer taxonomically valid, and the single anamorphic genus *Ceratorhiza* (Moore, 1987) appears to be the primary associate *P. leucophaea* (Zettler *et al.*, 2001).

The actual range of soil conditions tolerated by *Platanthera leucophaea* and the degree to which these habitat characteristics differ across its range are as yet unclear. Nevertheless, this species is the subject of recovery efforts that include establishment of new populations (U.S. Fish and Wildlife Service, 1999). Therefore, a better understanding is needed of factors that affect its distribution and potential for restoration. In this study, we compare soil characteristics of habitats occupied by this species with those of unoccupied potential habitats on the Illinois Till Plain. In particular, we ask whether this species occupies a gradient vs. a bimodal distribution of soil chemical and fertility conditions, and whether specific factors can be identified that correspond to its distributional limits.

MATERIALS AND METHODS

We analyzed physical, chemical and nutrient properties of 36 composite soil samples collected from 27 sites with habitats currently or formerly supporting *Platanthera leucophaea* populations throughout its range (Table 1). Most U. S. sites were located based on state

TABLE 1.—Number of collection sites and composite soil samples (in parentheses) analyzed for habitats associated with *Platanthera leucophaea*

Habitat	Illinois	Wisconsin	Michigan	Ohio	Ontario	Missouri	Virginia	Total
Silt loam prairie	6 (9)	3 (3)	—	—	—	—	—	9 (12)
Lake plain prairie	—	—	4 (4)	—	—	—	—	4 (4)
Sand prairie	—	3 (3)	2 (2)	—	2 (2)	—	—	7 (7)
Sedge meadow	—	—	—	1 (2)	—	1 (3)	1 (1)	3 (6)
Bog/Fen	—	1 (3)	1 (2)	—	2 (2)	—	—	4 (7)
Total	6 (9)	7 (9)	7 (8)	1 (2)	4 (4)	1 (3)	1 (1)	27 (36)

Natural Heritage Program data bases that identified specific locations with extant or formerly extant orchid populations. Twenty-three of these samples were obtained from prairie habitats derived from Wisconsinan-aged sediments in Illinois, Michigan, Wisconsin and Ontario. Following Bowles (1983), we classified samples from loess and glacial till as representing silty-clay loam prairies, and samples from more coarse-textured outwash or lake plain deposits as sand prairies or lake plain prairies, respectively. Additional samples included seven collections from peatlands classified as bogs in Wisconsin and Michigan, fens in Ontario and six collections from wetland sedge meadows in Ohio and unglaciated Virginia and Missouri. Although the Missouri habitat formerly supported this species, soil samples are from the original site mapped and described by Steyermark (1963) as a calcareous spring-fed meadow. Orzell & Kurz (1986) subsequently described this site as a Missouri prairie fen, but provided no soils data.

Soil samples comprised multiple random samples made to rooting depth (~15 cm) within specific orchid habitats (usually ~0.01 ha), which were combined into single composites for analysis. Within some sites, this procedure was repeated across moisture gradients occupied by *Platanthera leucophaea*, resulting in multiple site samples used for analysis. Samples were dried and then analyzed by the University of Wisconsin at Madison Soils and Plant Analysis Laboratory following methods of Page *et al.* (1982). Soil physical characteristics included % organic matter (OM) by thermal combustion and % of sand, silt, and clay by hydrometer method. Soil chemistry and nutrient assays included pH, cation exchange capacity (CEC) as meq/100 g and parts per million (ppm) extractable phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg) and manganese (Mn). Peat soils were highly organic and therefore were not analyzed for sand, silt or clay. For comparison with dried samples, a portable meter was also used to directly measure pH of ground water-saturated soil samples (~1:1 water:soil ratio) from the Missouri site ($n = 4$ samples), as well as two Ontario fens and one Wisconsin fen ($n = 9$ samples).

We compared the *Platanthera leucophaea* habitat data with Illinoian till plain soils by accessing data maintained on the National Soil Survey Center Soil Survey Laboratory Research Database. For this comparison, we used data sets representing three grassland soil associations developed in a loess depth gradient over weathered Illinoian till: the Hoyleton-Cisne-Huey Association (developed in 15–25 cm of loess), the Oconee-Cowden-Piasa Association (in 20–30 cm of loess) and the Herrick-Virden-Piasa Association (in 25–35 cm of loess) (Fehrenbacher, *et al.*, 1984). These soil associations extend from southeast to northwest across the Illinoian till plain, with the deeper Herrick and Virden soils entering the edge of the range of *P. leucophaea* (Fig. 2). We used data from the first two soil types listed for each association, which have <4% slope and would be most representative of potential orchid habitats. Comparable data available from the Soil Survey Database were pH, % OM (converted from

Organic Content by a factor of 1.7), CEC and % sand, silt and clay. In most cases, these data represented the upper 18 cm of the soil profile, which would be comparable to our soil samples. For final analysis, data for each variable were combined within soil associations because preliminary analyses found no significant differences among samples within associations for these variables.

To provide more information on potential habitat, we also collected and analyzed (as above) soil samples from two high quality prairie remnants available for *Platanthera leucophaea* restoration that are located on the Illinois Till Plain. The Anderson Prairie (Christian Co., Illinois) occurs on Oconee silt loam, while the Denby Prairie (Macoupin Co., Illinois) occurs on Keomah silt loam, which belongs to the Clinton-Keomah-Rushville association developed primarily under forest in deep loess (Fehrenbacher *et al.*, 1984). Both sites support populations of the ragged fringed orchid [*P. lacera* (Michx.) G. Don.], from which mycorrhizal fungi (*Ceratorhiza* spp.) have been isolated and found to be compatible with germinating *P. leucophaea* (L. Zettler). *Platanthera lacera* occurs within the range of *P. leucophaea*, but usually occupies more acidic soils and also ranges south on the Illinoian till plain (Sheviak, 1974).

To understand differences among known orchid habitats on mineral soils, as well as the Anderson and Denby Prairies, a Principal Components Analysis (PCA) was conducted on all soil textural, chemical and nutrient data using a correlation cross-products matrix, which gives variables equal weighting, on PCORD (McCune and Mefford, 1999; McCune and Grace, 2002). The significance of each axis was tested following Jackson (1993). A one-way ANOVA was used to compare differences among known orchid habitats on mineral soils and those on the Illinois Till Plain Cisne-Holyeton, Cowden-Oconee and Herrick-Virden soils groups. This ANOVA tested for differences in textural data, pH, % OM and CEC but not soil nutrients, which were absent from the Illinois Till Plain soils data. An orthogonal contrasts model was then used to compare all occupied vs. unoccupied habitats, with the Herrick-Virden soils excluded as they fall within the range of *Platanthera leucophaea.* A one-way ANOVA was also used to compare differences in soil nutrients among known habitats. The Newman-Keuls multiple-comparison test was used to determine which habitats differed (at $P < 0.05$) for each nutrient variable tested with ANOVA. All statistical analyses were conducted on NCSS software (Hintze, 2004). Peat soils from bogs and fens were excluded from statistical analysis and compared by inspection because they had extreme differences in soil characteristics from mineral soils.

RESULTS

The first two components of the PCA accounted for 65% of the cumulative variation among soils data and contained more information than expected by chance (Table 2). The third component accounted for 13.8% of the total variation and failed to contain more information than by chance by a difference of 0.054. The first component was highly positively correlated with increasing values for CEC, ppm Mg, Ca and K, % OM and % clay, reflecting the positioning of silty-clay loam prairies (Fig. 3). In contrast, most sand prairies corresponded to decreasing values of these factors, as well as lower percentages of silt and clay, and increasing % sand. Wisconsin sand prairies had stronger correspondence with positive factor loadings on the first axis, while lake plain samples from Michigan were more centrally located and associated with less sand content, higher pH and higher nutrient concentrations than sand prairies. On the second axis, most sedge meadows, as well as the Denby and Anderson prairies, corresponded to low values for % OM, CEC and most nutrients, and to higher values of Mn, silt and clay content. Alignment of sedge meadows on the third PCA axis (not shown) corresponded to high P and low pH values.

TABLE 2.—Variance extracted and linear (Pearson's r) and rank (Kendall's tau) correlations of soils variables with the Principal Components Analysis Ordination (Fig. 3)

	PCA axis					
	1		2		3	
% of variance	39.42		25.35		13.84	
Variable	r	tau	r	tau	r	tau
pH	0.392	0.263	−0.338	−0.131	−0.664	−0.613
% OM	0.571	0.418	−0.519	−0.223	0.492	0.292
ppm P	−0.048	−0.192	0.045	0.032	0.791	0.624
ppm K	0.747	0.535	0.234	0.246	−0.102	0.039
ppm Ca	0.853	0.682	−0.342	−0.153	−0.148	−0.110
ppm Mg	0.908	0.685	−0.143	−0.034	0.292	0.121
ppm Mn	−0.351	−0.327	0.569	0.253	0.240	0.353
% Sand	−0.508	−0.345	−0.839	−0.692	0.035	0.063
% Silt	0.366	0.271	0.814	0.678	0.036	0.044
% Clay	0.602	0.376	0.670	0.577	−0.135	−0.118
CEC	0.931	0.756	−0.269	−0.126	0.134	−0.004

Comparison of orchid habitats with soil characteristics of the Illinoian till plain revealed regional differences in soil texture, fertility and chemistry, and significant differences between existing and potential habitats (Table 3). As would be expected, % sand was higher in lake plain and sand prairies, while the percentages of silt and clay were lower in sand soils (Fig. 4a). However, silt content reached maximum values on Illinoian till plain soils while clay was highest in silty-clay loam soils. Fertility, as indicated by CEC, co-varied with % OM ($r = 0.71$), with highest values in silt loam prairies and lower values on the Illinoian till plain (Fig. 4b). The Herrick-Virden soils had CEC values similar to those of sedge meadow orchid habitats. Silty-clay loam and lake plain prairie habitats tended to be circum-neutral, and sedge meadows and Herrick-Virden soils slightly more acid (Table 3). Among mineral soil habitats supporting *Platanthera leucophaea*, silty-clay loam soils had higher K, Ca and Mg concentrations while Mn was higher in sedge meadows. Bog and fen habitats were strongly acid with high organic content and high nutrient concentrations in comparison to habitats on mineral soils (Table 3). Direct measures of pH from saturated soil samples from the Missouri site averaged 6.125 (±0.04 SD), while dried samples averaged 6.53 (±0.18 SD). Direct pH measures from the Ontario and Wisconsin fens averaged 6.16 (±0.23 SD), while dried samples averaged 5.92 (±0.16 SD).

DISCUSSION

Habitat gradient.—*Platanthera leucophaea* occurs across a complex gradient of soil base concentrations, as expressed by CEC and concentrations of Ca and Mg. This species occupies circum-neutral base-rich organic soils of Illinois and Wisconsin silty-clay loam prairies, less base rich but more alkaline soils with lower organic content on Michigan lake plain habitats and moderately acid and more nutrient poor sand prairies and sedge meadows that often occur as outliers. Bogs and fens in the eastern part of this species range tend to be more strongly acid and highly organic. Much of the variability in base content of mineral soil habitats may be due to organic content, as indicated by the high correlation between CEC and % OM. Thus, the high base concentrations in Illinois and Wisconsin prairie habitats reflect the high organic content typical of these mollisols. The higher pH

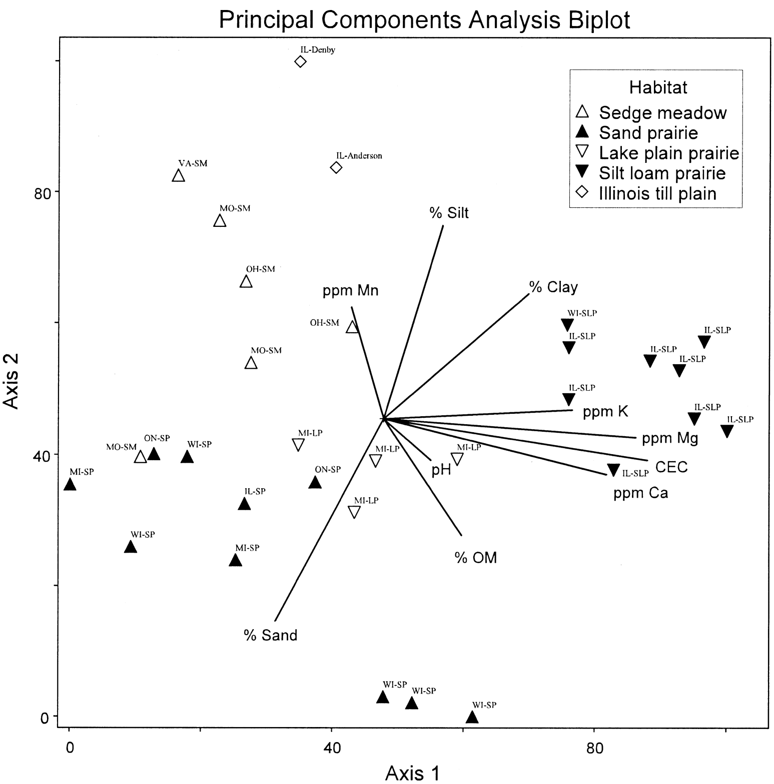

FIG. 3. Principal Components Analysis ordination biplot of *Platanthera leucophaea* habitat soil characteristics Abbreviations represent states or provinces (IL = Illinois, MI = Michigan, MO = Missouri, OH = Ohio, ON = Ontario, VA = Virginia) and habitats for sedge meadows (SM), sand prairies (SP), loam sand prairies (LSP), silt loam prairies (SLP) and potential Illinois Till Plain habitat represented by Denby and Anderson prairies. Angle and length of vectors is proportional to strength of axis correlations. *See* Table 2 for all variables and percent of variance extracted for Principal Components

values and lower nutrient concentrations of lake plain habitats in Michigan may result from comparatively low organic matter content in a calcareous soil matrix on lake plain substrates. In this situation, the high pH also may increase availability of ions in the soil solution. Nevertheless, *P. leucophaea* also occupies more acidic sand prairies and sedge meadows with relatively low nutrient availability, and thus appears tolerant of a wide range of soil conditions.

Given the range of mineral soil conditions that *Platanthera leucophaea* occupies, its occurrence in moderately acidic bogs and in fens is not surprising. Although the peat soils of these habitats had extremely high base concentrations, most nutrients are bound in OM in peat soils and are not available for plant uptake, especially under acidic conditions (Verhoeven, 1986; Vitt and Chee, 1990). Some factors may alleviate these conditions. For example, mycorrhizal fungi may increase efficiency of mineral uptake in peat soils and could provide a competitive advantage, as well as a favorable germination site, for orchids in these habitats (Rasmussen, 1995). Because our primary analysis was based on dried soil samples, we cannot resolve the full degree to which groundwater flow might have affected these

TABLE 3.—Comparisons of soil characteristics among habitats supporting *Platanthera leucophaea*, indicated by asterisk (*), and potential habitats. ANOVA probabilities are one-way comparisons of soil structure and chemistry variables among potential and existing habitats (ANOVA 1) and soil nutrient variables among existing habitats (ANOVA 2). Orthogonal contrast probabilities are comparisons between extant habitats and potential habitats, excluding Herrick-Virden soils (*see* text). Soil nutrient variables with similar lower case letters are not different with Neuman-Keuls multiple comparison test at P <0.05. Bog and Fen samples are excluded from ANOVA. Anderson and Denby samples represent single measures

		ANOVA 1						ANOVA 2				
Soil/Vegetation	Metric	% Sand	% Silt	% Clay	CEC	pH	% OM	ppm P	ppm K	ppm CA	ppm MG	ppm Mn
Silt-loam	mean	16.22	57.56	26.22	32.56	6.90	10.39	10.58	190.89	4127.56	1396.89	17.22
Prairie*	SE	3.04	4.02	2.80	0.94	0.09	0.70	2.83	23.64	132.74	39.28	5.51
										a,b		a
Lake-plain	mean	47.00	41.00	12.00	20.50	7.43	6.13	2.45	92.25	4050.00	462.00	8.75
Prairie*	SE	3.56	4.65	3.51	2.36	0.13	0.79	1.75	15.96	389.68	119.68	1.38
									a	a,b,c	a	a
Sand	mean	72.50	25.20	2.30	20.30	6.47	9.95	10.53	74.40	2861.10	697.20	21.50
Prairie*	SE	2.60	2.50	0.54	3.33	0.19	1.52	0.96	8.39	405.74	153.54	2.81
									a	b,c,d	a	a
Sedge	mean	31.50	55.33	13.17	14.17	6.23	7.30	9.95	89.17	1930.50	517.00	80.50
Meadow*	SE	8.28	5.55	3.18	2.17	0.22	0.51	1.54	13.90	329.74	87.48	21.33
									a	c,d	a	
	P							0.0983	<0.0001	0.0003	<0.0001	0.0002
Herrick	mean	6.37	74.71	18.89	15.01	5.98	2.67	—	—	—	—	—
Virden	SE	0.54	1.89	1.67	0.78	0.17	0.16	—	—	—	—	—
Oconee	mean	5.96	79.93	14.11	11.44	6.51	2.05	—	—	—	—	—
Cowden	SE	0.57	1.25	0.97	1.09	0.15	0.11	—	—	—	—	—
Cisne	mean	11.71	71.80	16.58	11.04	6.39	1.89	—	—	—	—	—
Hoyleton	SE	0.88	1.14	0.50	0.50	0.15	0.12	—	—	—	—	—
ANOVA	P	<0.0001	<0.0001	<0.0001	<0.0001	0.0012	<0.0001					
Orthogonal	P	<0.0001	<0.0001	0.15431	<0.0001	0.0595	<0.0001					
Bog & Fen*	mean	—	—	—	64.00	6.00	83.96	72.46	1235.00	8768.14	2365.14	60.71
	SE	—	—	—	6.99	0.13	2.49	9.55	523.72	729.14	297.84	28.69
Anderson	—	18.00	64.00	18.00	16.00	6.80	4.70	8.00	71.00	2540.00	430.00	150.00
Denby	—	8.00	62.00	30.00	11.00	5.00	2.70	13.00	107.00	1430.00	460.00	92.00

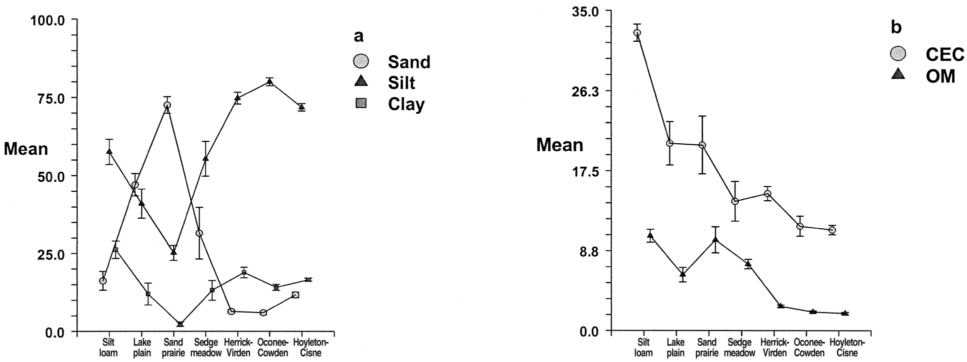

FIG. 4.—Variation in a) soil texture (% sand, % silt and % clay) and b) CEC and % OM among silt-loam prairie, lake plain prairie, sand prairie, sedge meadow habitats and Illinoian till plain soils. Connecting lines indicate regional gradients among categorical variables

habitats. However, our groundwater-saturated soil pH data do not support contentions that these habitats are buffered by minerotrophic groundwater that increases pH values and Ca concentrations available to plants (*e.g.,* Steyermark, 1963; Schwintzer, 1978; Orzell and Kurz, 1986). Ford (1985) also found no evidence for strongly calcareous conditions in Ontario fen habitats for this orchid. To some extent, the acidity-alkalinity gradient in peat soils may correspond to water chemistry (Vitt and Chee, 1990; Bragazza and Gerdol, 2002), which would also suggest that our study sites did not have strongly alkaline groundwater. Our samples also provide no direct evidence that *P. leucophaea* plants root in a more calcareous substrate in bogs, as suggested by Correll (1950) and Sheviak (1974). More work is needed to understand the edaphic environment and nutrient availability to *P. leucophaea* in bogs and fens, as well as the potential for successional change or stability in bog mats to effect persistence of this species (*e.g.,* Case, 1987).

Limits to the distribution of Platanthera leucophaea.—Our finding of a complex habitat gradient occupied by *P. leucophaea* indicates that this species does not occupy a strongly bimodal distribution with respect to soil chemistry or fertility. However, our analysis of CEC tends to support Sheviak's (1974) hypothesis that the limit to the southern distribution of this species in tallgrass prairie corresponds to a shift to lower base concentrations on the Illinois Till Plain, and that these conditions are moderated in deeper loess within the range of *P. leucophaea* on Virden and Herrick soils. Nevertheless, other characteristics of Illinois Till Plain soils may affect this distribution. Their extremely low organic content and high silt content suggests that they have comparatively low soil moisture holding capacity (Larcher, 1975). Because *P. leucophaea* is sensitive to drought (Bowles *et al.*, 1992), soil moisture holding capacity of these soils could therefore fall below a threshold for survival of this species. In contrast, the nutrient-poor outlier habitats for this orchid are wetlands with greater % OM, which could buffer against moisture loss during drought.

Other limits to the habitat gradient for *Platanthera leucophaea* are less clear, but appear to include conditions found in midwestern prairie fens. These highly calcareous fens contain many prairie plants, including the white lady's slipper orchid (*Cypripedium candidum* Muhl. ex Willd.), but have not been found to support *P. leucophaea* (Sheviak, 1974; Moran, 1981; Bowles, 1983). Calcium concentrations in these fens reach 20,000–40,000 ppm (Carpenter, 1995). This represents an order of magnitude higher concentration of Ca than in habitats supporting *P. leucophaea.* Such conditions, along with high alkalinity, could be investigated as a principal cause for the absence of this orchid from calcareous fen habitats, as highly calcareous soils are known to exclude some plant species (Larcher, 1975).

It is unknown whether the ecological amplitude displayed by *Platanthera leucophaea* has a genetic or phenotypic basis. Tolerance of a wide range of soil conditions may not be unusual for widespread prairie species. Mead's milkweed (*Asclepias meadii* Torr.) habitats vary from calcareous base rich prairie soils to acidic nutrient poor soils of glades, yet this species has little measured genetic differentiation among populations, and plants from different seed sources grow equally well in neutral soils (Bowles *et al.*, 1998; Tecic *et al.*, 1998).

Potential mycorrhizal interactions.—Understanding soil effects on the distribution of *Platanthera leucophaea* must take into account whether edaphic factors may affect the distribution of its mycorrhizal fungi, as reported for vesicular-arbuscular fungi (Johnson *et al.*, 1991; Johnson *et al.*, 1992; Gibson and Hetrick, 1988). However, little specific information is available on the soil requirements, host specificity and distribution of orchid fungi (Rasmussen, 1995). Fungal strains of the anamorphic genus *Ceratorhiza* (Moore, 1987) have been frequently recovered from *P. leucophaea* in mature plants (Zettler *et al.*, 2001) and protocorms alike (Piskin *et al.*, 2003), suggesting that this genus is the primary associate of this orchid, at least in Illinois. It is conceivable that *Ceratorhiza*'s prevalence in *P. leucophaea* habitats may be linked to the high organic content of prairie soils due to the genus' ability to produce cellulase and pholyphenol oxidase – enzymes active in the breakdown of cellulose and woody debris, respectively (Zelmer *et al.*, 1996; Rasmussen, 2002). Nevertheless, isolation of *Ceratorhiza* from *P. lacera* in Illinois Till Plain habitats, as well as its compatibility with *P. leucophaea* seedlings suggests that soil conditions may not directly affect these soil fungi and therefore may affect *P. leucophaea* directly rather than indirectly through its mycorrhizal fungi. However, this conclusion remains conjectural until research reveals the degree to which interspecific variation, as well as edaphic adaptation, occurs in *Ceratorhiza* across edaphic transitions thought to be barriers to orchid distribution.

Implications for establishing new populations.—Our results suggest that potential for success in establishing *Platanthera leucophaea* can be guided and evaluated through soils analysis. Optimum tallgrass prairie habitat for this species is circum-neutral with relatively high organic content and nutrient concentrations. Higher alkalinity may provide suitable conditions in sand habitats with lower organic content. More acid sites may require constant soil saturation, as well as high % OM, such as in sedge meadows, bogs or poor fens. Less optimum conditions that might be avoided appear to include acidic nutrient poor soils with low organic content and high silt content. For example, the PCA ordination and soils analyses suggest that the Denby Prairie is very marginal with respect to the ecological amplitude of this species because of its low pH, low CEC and low % OM. Because these measures are higher for the Anderson Prairie, it appears to be more suitable for this species. However, both sites have high % silt content and low % OM in comparison to *P. leucophaea* habitats on Wisconsinan-aged soils, which suggests that their potential for sustaining restored *P. leucophaea* populations could be reduced by high vulnerability to drought. Among the Illinoian till plain soil types we examined, the Virden-Herrick soils appear most appropriate for *P. leucophaea* because they are developed in deeper Wisconsinan-aged loess with higher % OM and CEC, and indeed occur within the range of *P. leucophaea.* Acidic or nutrient poor soils may not only be problematic for establishing this orchid near the southern boundary of its range, but also in areas with low organic content north of the Wisconsinan glacial boundary, such as inland sand areas.

An understanding of orchid mycorrhizal fungi soil requirements, as well as host specificity, and how soil chemistry affects germination, are also needed to provide a more clear understanding of requirements for establishing *Platanthera leucophaea* (Zettler *et al.*, 2001).

Research is also needed to learn whether habitat variation corresponds to genetic differentiation in *P. leucophaea*. For example, are orchid populations occupying acidic nutrient poor habitats, such as bogs or sedge meadows, genetically adapted to these conditions and are they, therefore, most appropriate for establishment into other habitats in which soil conditions appear to be marginal for this species? Clearly, other biological factors, such as competition from dominant prairie grasses and their interactions with mycorrizal fungi, as well as disturbance processes that promote seedling establishment, may also affect the local distribution and restoration potential of this species.

Acknowledgments.—We thank the Illinois Department of Natural Resources, Illinois Nature Preserves Commission, Michigan Natural Features Inventory, Ohio Department of Natural Resources, Virginia Natural Heritage Program, Missouri Department of Conservation and Department of Natural Resources and the Wisconsin Department of Natural Resources and Scientific Areas Council, for permission to sample soils, as well as Bil Alverson, Dan Brouillard, Fred Case, Don Kurz, Randy Nyboer, Steve Packard, Paul Pratt, Ralph Ramey, Tim Smith, Tom Wieboldt and Roger Troutman for field assistance. We thank J. Ross Brown, Vivian Brownell, Paul Catling, Bruce Ford and Sheila McKay for assistance in locating Canadian populations. We also thank the Natural Land Institute, James Woodworth Prairie Preserve – University of Illinois at Chicago, and U.S. Fish and Wildlife Service for funding support, and Robert Darmody, Christopher Dunn, Rita Hassert, Karel Jacobs, Richard Jensen, Jenny McBride, Charles Sheviak and anonymous reviewers for valuable time and assistance with preparing and revising this paper.

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SUBMITTED 28 JUNE 2004 ACCEPTED 5 APRIL 2005