A VEGETATION ANALYSIS OF TALLGRASS PRAIRIE IN SOUTHERN ONTARIO

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Abstract. The purpose of this study is to describe the composition of tallgrass prairie in southern Ontario and compare floristic variation with stands to the west in the prairie-forest border. Sixty three stands were located, most on sand plains. Direct gradient analysis and ordination were used to analyze trends of vegetation and environmental factors. Stands were dominated by prairie grasses, especially *Andropogon gerardii* and *A. scoparius*. Species responses along the moisture gradient often resembled Gaussian distributions. Ordination by detrended correspondence analysis supported the use of soil moisture as the primary gradient since the first DECORANA axis was strongly correlated with soil water retaining capacity, as well as texture, organic matter, depth of A horizon, fire frequency, magnesium, calcium, percent sand, and stoniness. Six prairie types are described using a moisture-substrate classification. Prairie communities in southern Ontario appear to require sandy to sandy-loam soils and periodic burning and/or xeric conditions. Inter-regional comparisons of prevalent species lists indicate wetter Ontario prairies are most similar to Michigan lakeplain prairies, whereas drier prairies are most similar to Michigan's woodland prairies and mesic sand prairies and Wisconsin's savannas. Typical dominants of drier Midwest prairie, such as *Bouteloua curtipendula*, *Sporobolus heterolepis*, and *Stipa spartea* are rare in Ontario, reflecting in part a shift in the underlying moisture gradient, as well as differences in soils and physiography.

INTRODUCTION

Scattered areas of tallgrass prairie occur in the deciduous forest region of southern Ontario, often associated with oak or oak-hickory savanna (Bakowsky 1988). These plant communities are similar to others in the prairie-forest border to the west (Gleason 1917, Curtis 1959, Anderson 1983). Their occurrence in southern Ontario gives rise to questions of origin, composition, present habitat characteristics and relations to other vegetation types.

Pollen evidence indicates that many prairie species were present in the prairie-forest border since at least the end of the Pleistocene (Benninghoff 1964), but did not form a distinct assemblage until the Xerothermic, about 8,000 years ago (King 1981). The effects of this climatic change were quite widespread and may have included areas in southern Ontario (Riley and Bakowksy, in prep.). Maps of the "prairie peninsula" produced by Transeau (1935, Stuckey 1981) suggest that prairie vegetation may have extended as far north and east as southwestern Ontario (Transeau made no mention of finding any such vegetation, but he may not have visited southern Ontario, R.L. Stuckey, personal communication). Prairie species may have dispersed into southern Ontario from the southwest (Illinois, Michigan) and southeast (Ohio) (Curtis 1959, Pringle 1982).

The presence of prairies in southwestern Ontario prior to European settlement can be demonstrated with survey records (Lumsden 1966, Pratt 1979, Faber-Langendoen and Maycock 1987). Sites further east were often referred to as "plains" or "oak plains", especially along the Lake Ontario shoreline and in Brant County (Lizars 1913, Wood 1961, Langendoen and Maycock 1983, Szeicz 1989). The discovery in Brant County of *Quercus ellipsoidalis*, an oak typical of oak barrens and oak savanna (Curtis 1959, White 1983), separated by 400 km from its nearest population in Michigan, is further evidence of the open habitat that prevailed up to the time of settlement (Ball 1981). Other studies describe localities where prairie communities existed prior to settlement (Rodgers 1966, Roberts et al. 1977, Reznicek 1980, Reznicek 1983, Reznicek and Maycock 1983, Stewart 1984, Catling et al. 1992).

More recent studies of prairie vegetation in the midwest have used gradient analysis to focus on vegetation-environment relations and species distributions (Curtis 1955, Dix and Smeins 1967, White and Madany 1981, Nelson and Anderson 1982, White and Glenn-Lewin 1984).

In this study, we analyze the prairie vegetation of southern Ontario using gradient analysis to determine the vegetation and environment features of these sites. Community types are identified and compared with other prairie areas in the upper Midwest in order to clarify the compositional characteristics of Ontario prairies.

Study Area

Climate

The climate of extreme southern Ontario varies significantly between Essex county in the southwest and the central highlands region of Waterloo, Middlesex and Brant counties. The differences between Essex and Waterloo counties for a number of climatic factors are as follows (from Environment Canada 1970):

mean annual temperature °C,	Essex	10	Waterloo	6
January isotherm °C,	"	-4	"	-6
July isotherm °C,	"	23	"	19
annual precipitation (cm),	"	69	"	91
annual snowfall (cm),	"	89	"	178

Southwestern Ontario occurs within the B4 Humid Zone of Thornthwaite and Mather (Sanderson 1948), which also includes Wisconsin, Illinois, Missouri, Michigan, parts of Indiana and northwest Ohio. The moisture index for this zone indicates that water deficits may occasionally occur, but are less probable further east. Exposed ridges, south and west facing slopes, and broad unprotected sand plains are affected by the warmer than normal microclimates associated with the Great Lakes (Hills 1952, Chapman and Brown 1966).

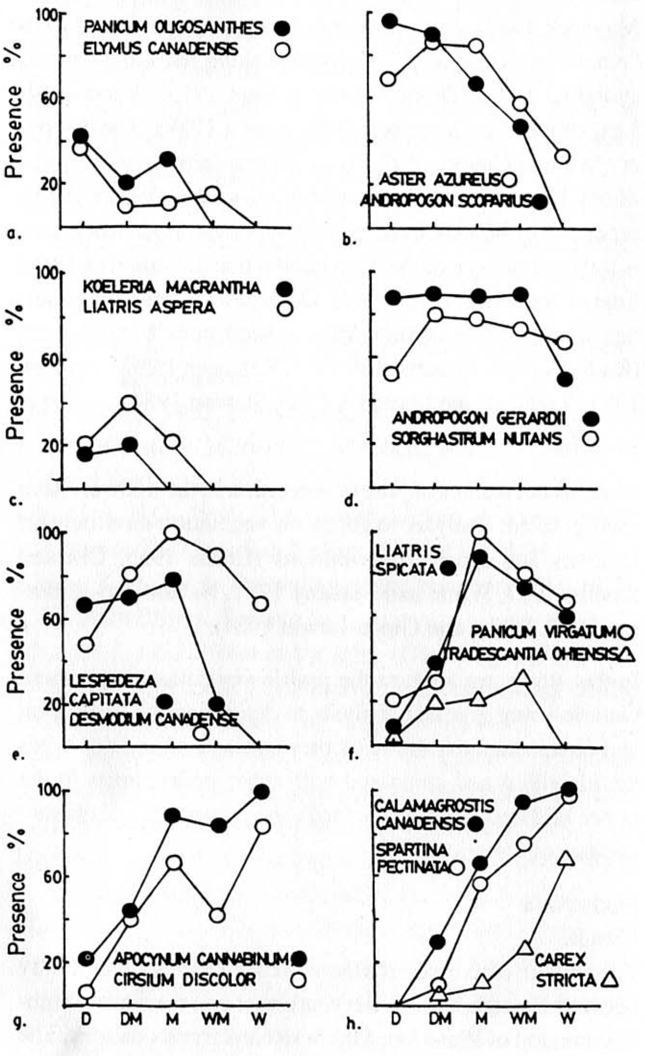

Figure 1. Representative species response curves along the moisture gradient from dry to wet in southern Ontario. Species abundance is measured as the percent presence within a moisture segment.

Physiography and soils

Almost all stands containing tallgrass prairie are located on sand plains formed as deltaic or beach deposits of 150-200 m elevation following Wisconsin glaciation (Terasmae 1980). Soils vary from coarse-textured sand at Sarnia, to silty/sandy loams at Walpole Island, to very fine sands at Turkey Point. The central highlands (360 m elevation), with more varied topography, are fringed by an extensive morainal system of till plains (Chapman and Putnam 1966). Stands of the central highlands occur on sandy loam soils over rocky substrate of the Galt and Paris till moraines and occur on steeper slopes than stands on the sand plains.

A number of stands are located along or near railways, including those at Brights Grove (railway built in 1860), many near Dumfries (railways built in 1890's) and many near the Lake Ontario shoreline (railways built in 1850's-1870's).

METHOD

Data collection

Stands were selected in 1981 and 1982 on the basis of visual dominance of grasses and forbs typical of tallgrass prairie (Weaver and Fitzpatrick 1934, Curtis 1959, Langendoen and Maycock 1983). Sixty three stands, representing a range of moisture and topographic conditions, were included (see Langendoen and Maycock Figure 1). Forty of the 63 stands had minimal human disturbance caused by plowing, grazing, or soil disturbances from railway right-of-way activities. We compiled a complete vascular plant species list for each of the 63 stands in both June and August-September. In the 40 undisturbed stands, 15 meter square quadrats were randomly laid in August and September, and species frequency and cover were recorded. In June, if spring ephemerals were abundant, 15 quadrats were laid to estimate their cover.

Soil pits 0.5 m in depth were dug to describe soil profiles in all stands. Field pH was measured with a Cornell pH test kit. Samples were collected from both A and B horizons for nutrient, moisture, texture and organic matter analyses. Stands were also visually assessed for incidences of fire and other disturbances, as well as site moisture and stoniness. Fire varied from 1 (no evidence) to 5 (burned annually during 1981-83); stoniness varied from 1 (sandy, pebbly) to 5 (rocks greater than 25 cm). A five point site-moisture classification ranging from wet to dry was determined on the basis of topographic position, substrate and degree of standing water in spring.

Soils were air-dried, broken to primary particle size and passed through a 2 mm sieve. Duplicate samples were sent to the Ontario Soil Testing Laboratory at Guelph for analyses of phosphorus, potassium, magnesium, calcium and pH. Due to costs, magnesium and calcium analyses were cut off above

Table 1. Summary of species cover values for the 5 segments of the moisture gradient. Only species attaining at least 5% cover in any one type are included.

Species	Dry	Dry-Mesic	Mesic	Wet-mesic	Wet
Poa compressa	6	6	3		
Andropogon scoparius	46	31	6	2	
Hieracium florentinum	1	8			
Carex pensylvanica	2	7	3		
Aster azureus	2	6	2	1	
Solidago juncea	1	9	8	3	
Sorghastrum nutans	5	4	6	6	1
Andropogon gerardii	14	14	14	15	2
Coreopsis tripteris			5	3	
Desmodium canadense	1	1	6	3	1
Panicum virgatum		2	6	12	1
Fragaria virginiana		1	2	5	
Pycnanthemum virginianum		1	5	6	6
Calamagrostis canadensis		4	9	8	30
Solidago canadensis		1	4	10	6
Spartina pectinata			1	4	22
Aster simplex			1	1	9
Carex sartwellii				2	9
no. stands (select)	11	5	6	12	6

(Community Type)

200 and 2000 ppm respectively, and nitrogen was analyzed in only 15 stands selected to represent the range of moisture conditions. Nitrogen was measured using the micro-Kjeldahl method. Loss on ignition at 600 °C for 4 hr was used to measure percent organic matter content. Texture of the soil fraction <2mm was determined by the hydrometer method. Hilgard cups filled with oven-dried soil were soaked until thoroughly saturated and subsequently dried for 24 hr at 105 °C to determine soil water retaining capacity, calculated as the ratio of the difference between wet and dry weights to dry weight.

Plant nomenclature follows Fernald (1950) for the dicots, Dore and McNeill (1980) for the grasses, and Voss (1972) for the remaining monocots. The vouchers have been deposited in the herbarium of the Ecology Laboratory, Erindale College, University of Toronto.

Data analyses

Percent presence (%P) was first calculated for each species across all 63 stands. Presence provides an indication of the floristic character and homogeneity of the stands because it measures the ubiquity of the component species (Curtis and Greene 1949). Frequency and average cover were calculated from quadrat data in the 40 select stands, and also averaged over all stands.

The site-moisture designations were used to organize the stand data into community types. We recognized 5 segments of a moisture gradient: dry, dry-mesic, mesic, wet-mesic and wet. We employed this site-type classification to facilitate comparisons with other regions (see below), and because a similar method is being used as part of a larger study of the vegetation of Ontario. Percent presence, mean frequency and mean cover were averaged for all stands within a segment of the gradient. Species abundances for each segment were then organized as prevalent species lists (Curtis 1959) as follows: first, the average number of species per stand within a segment was determined. Species were then arranged in decreasing order according to their presence values. The limit to the number of species on the list was determined by the average number of species per stand. For example, the 19 dry stands had an average of 59 species per stand (Appendix 1); hence the prevalent list includes the top 59 species, from 100% presence on downward. Environmental factors were also summarized for each segment.

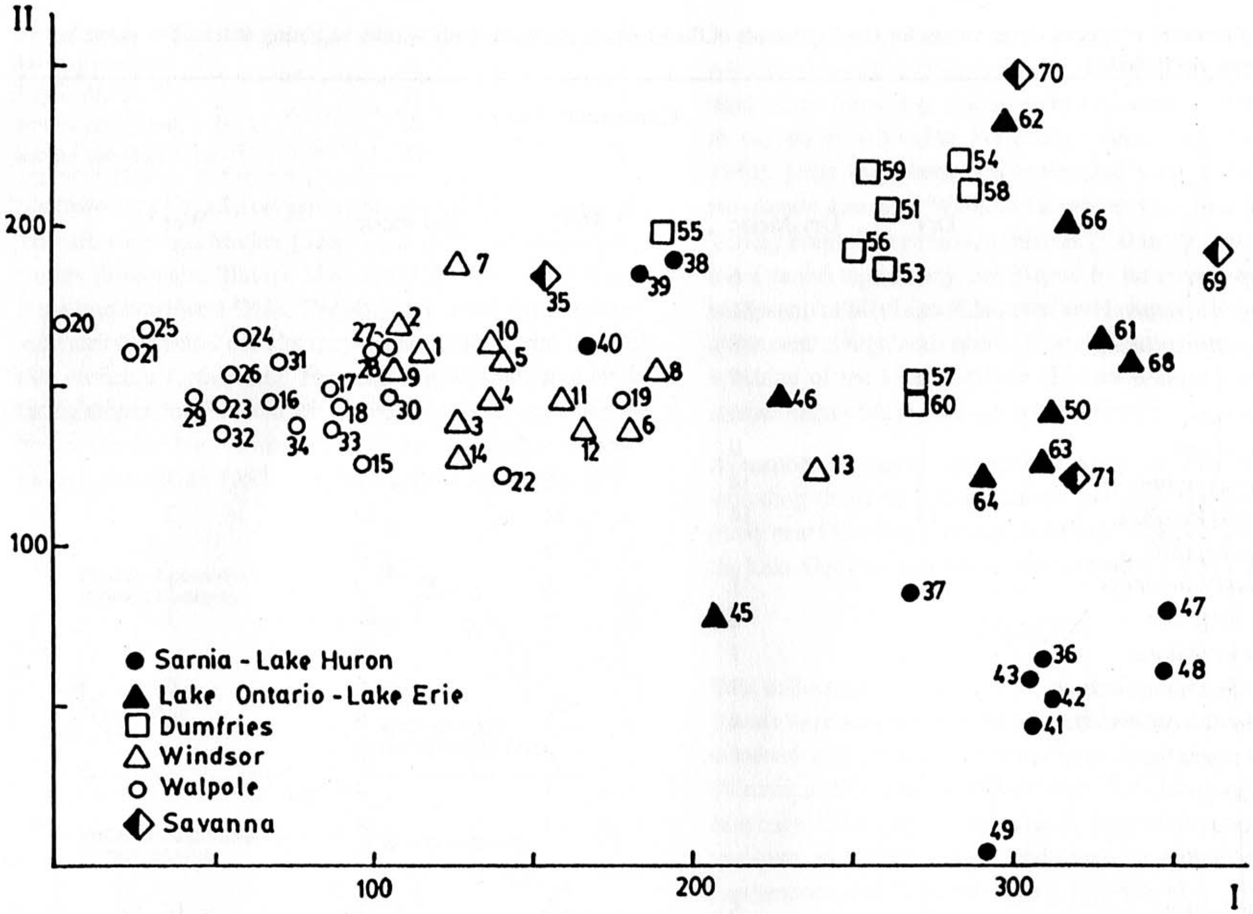

Figure 2. Detrended correspondence analysis of 63 prairie stands using species presence. Position of the 63 stands (and 4 savanna/woodland stands) on axis 1 and axis 2 is indicated by regional identifier. Numbers refer to stand locations (see text).

Detrended Correspondence Analysis (DECORANA) was used to analyze major compositional trends (Hill and Gauch 1980). DECORANA is especially useful for large, heterogeneous data sets that have strong primary gradients. The ordination model assumes a unimodal species response along gradients (Austin 1985, Minchin 1987, Peet et al. 1988). The first ordination matrix contained presence data for 322 species in 63 stands (and 4 savanna/woodland stands). The second ordination contained mean frequency data of 225 species in 40 stands and was used to test vegetation-environment relationships using Spearman rank correlations of DECORANA axes with environmental factors. Both ordinations only included species with occurrences in more than 2 stands.

Community comparisons with other regions

Data for Wisconsin prairies and sand barrens (6 types) (Curtis 1959) and Michigan prairies (7 types) (Chapman 1984) have been summarized by prevalent species lists using segments of a moisture gradient similar to that of Ontario. Prevalent species lists of Ontario prairie were first compared with these regions using the Index of Similarity developed by Sorenson (1948, in Mueller-Dombois and Ellenberg 1974). Second, a matrix of the prevalent species lists was ordinated. The matrix, which consisted of constancy values for 304 species in 18 types, was analyzed using default settings in DECORANA.

RESULTS

Composition summary

A total of 503 vascular plants were recorded in the 63 stands of Ontario prairies. Grasses were most dominant and *Andropogon gerardii* had the highest percent presence (87%) and an average cover of 13%. Other grasses with high cover values included *Andropogon scoparius* (18% cover), *Calamagrostis canadensis* (9%), *Panicum virgatum* (5%), *Spartina pectinata* (5%), *Sorghastrum nutans* (5%) *Poa compressa* (3%), and *Poa pratensis* (3%). A variety of forbs had high average cover values, including *Solidago canadensis* (5%), *Pycnanthemum virginianum* (4%), *Fragaria virginiana* (3%), *Desmodium canadense* (3%), and *Solidago juncea*

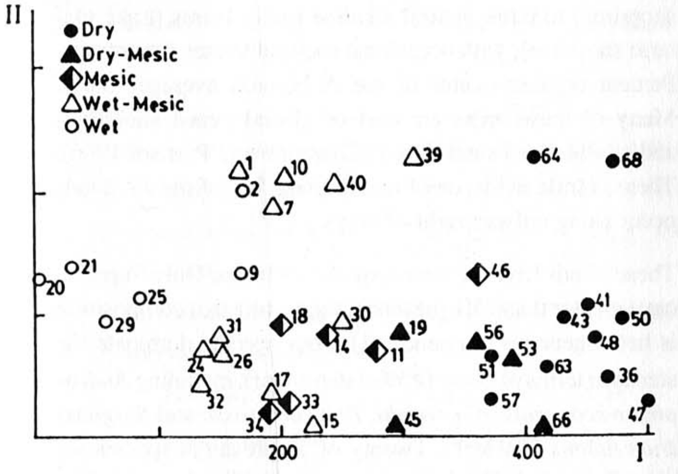

Figure 3. Detrended correspondence analysis of stands using frequency. Position of the 40 stands on axis 1 and axis 2 is indicated with symbols that refer to site-moisture designations.

(3%). Ten of the 13 species with high cover species belonged to the Poaceae or Asteraceae.

Woody plants were of minor importance in the prairies, the only widespread species being the vine *Vitis riparia* and the shrub *Cornus racemosa*. None were frequent, except locally. The tree species of highest constancy was *Quercus velutina* (38%), found most often as a seedling or sprout.

Direct gradient analysis

Presence values were plotted along the moisture gradient for several species (Figure 1). Species dominant in dry or dry-mesic stands but which occurred commonly in other moisture conditions include *Andropogon scoparius* and *Aster azureus* (Figure 1b). Several species had optima in dry or dry-mesic stands, but were of low presence and restricted to this part of the moisture gradient, e.g. *Koeleria macrantha* and *Liatris aspera* (Figure 1c).

Andropogon gerardii and *Sorghastrum nutans* had broad responses and no clear moisture preference, though they were less often found in wet stands (Figure 1d). Others, such as *Desmodium canadense*, *Lespedeza capitata*, *Liatris spicata* and *Panicum virgatum*, were most often found in mesic stands (Figure 1e,f).

Broad ranging species most often found in wet or wet-mesic stands included *Tradescantia ohiensis* (Figure 1f), *Calamagrostis canadensis*, *Spartina pectinata*, and *Carex stricta* (Figure 1h).

Species responses along the moisture gradient often resembled bell-shaped distributions. However, several species showed deviations from this pattern, including *Elymus canadensis* and *Panicum oligosanthes* in the drier stands (Figure 1a) and *Apocynum cannabinum* and *Cirsium discolor* in the wetter stands (Figure 1g). These trends were also observed when mean frequency values are used.

Dominance patterns using species cover are summarized for each moisture segment in Table 1. Prairie grasses dominate in all moisture conditions. Species richness per stand was highest in mesic stands and lowest in the dry. Stand richness (Appendix 1) and number of dominants appear to be inversely related.

Ordination

The DECORANA ordination of all 63 stands tended to group stands based on a combination of regional location and site-moisture characteristics (Figure 2). Walpole stands are separated at one end of the axis, blending somewhat with the intermediately-placed Windsor stands. All other stands are placed at the other end, but they separated strongly along the second axis of the ordination. The regional patterns retained on the ordination may reflect both distinct differences in habitat and the isolation of these prairie areas from each other.

The DECORANA ordination of select stands by species frequency is presented in Figure 3, with stands labelled according to their site-moisture designations. Stands segregated along the first axis on the basis of species composition relating to a site-moisture gradient. There was some overlap between adjacent site-moisture groups, especially for mesic and wet-mesic stands. Species locations in ordination space were comparable to their position along the direct moisture gradient (Figure 1).

Second axis variation was especially apparent among the wet-mesic stands, where 5 stands from Windsor and Sarnia (1,7,10,39,40) were separated as a group from 7 other wet-mesic stands at Walpole (15,17,24,26,30,31,32) (Figure 3). Species located in similar ordination space with the Windsor-Sarnia stands were *Potentilla simplex*, *Vitis riparia*, *Fragaria virginiana*, *Apios americana*, *Cirsium discolor*, *Carex lanuginosa*, and *Solidago canadensis*. Those associated with Walpole stands included *Aster dumosus*, *Carex meadii*, *Panicum virgatum*, *Juncus balticus*, *Viola papilionacea*, *Zizea aurea*, *Lysimachia quadriflora*, *Eleocharis elliptica*, *Liatris spicata*, and *Hypoxis hirsuta*. Dominance by *Carex foenea* and *Festuca spp.* accounted for the separation of the two dry stands (64, 68) from all the others (Figure 3).

Table 2. Spearman rank correlations between first 2 axes of detrended correspondence analysis and environmental variables.

Environmental variable	Axis 1		Axis 2
Soil water retaining capacity	-.63	*	.22
Percent sand in B horizon	.54	*	.28
Texture	-.60	*	-.30
Organic Matter	-.40	*	.26
Depth of A horizon	-.78	*	.14
pH	-.20		-.28
Fire	-.68	*	-.05
Stoniness	.53	*	-.28
Phosphorus	-.18		.25
Potassium	-.06		.03
Magnesium	-.70	*	.02
Calcium	-.44	*	-.06

* p <0.05

Environmental gradients

Soil water retaining capacity, texture, organic matter, depth of A horizon, fire, magnesium and calcium were negatively correlated and percent sand and stoniness were positively correlated with the first DECORANA axis ($p \leq 0.05$) (Figure 3, Table 2).

No factors were significantly correlated with the second DECORANA axis, although texture and percent sand were significant at the $p < 0.1$ level. When percent sand in the B horizon was plotted over the ordination, changes were most significant along the first axis, as expected, but notable differences also occurred between the two wet-mesic groups that were separated on the second axis. These differences may account for the vegetational changes observed between Windsor-Sarnia prairies and Walpole prairies (Figure 3). When percent sand values were compared between these two groups, their distributions were significantly different (U_s=35, $p < 0.01$). Mean values for Windsor-Sarnia were 88 ± 6% and for Walpole were 57 ± 17% (Table 3). Field pH and fire index were also higher for Walpole prairies (Table 3).

Prairie types

Six prairie types were designated based on the results of the direct gradient analysis and ordination. We used the five moisture segments, with the wet-mesic segment divided into sandy and sandy loam sub-types, and two wet stands reassigned to the wet-mesic sandy type (see Figure 3). Environmental factors are summarized for the six types in Table 3.

Dry prairie

The dry prairie stands are widely scattered in southern Ontario, and occur on well drained slopes or upland stands. Soils vary from coarse, slightly acidic sand (Sarnia-Lake Huron shoreline) to more neutral alkaline sandy loams (Lake Ontario shoreline), with occasional rock substrates (Dumfries). Percent organic matter of the A horizon averages 5.6%. Many of these areas are part of glacial beach shorelines and/or stabilized sand dunes (Chapman and Putnam 1966). There is little evidence of recent fires. Ten of the 19 stands occur along railway right-of-ways.

These stands have the lowest species richness. Only 5 species have greater than 75% presence, suggesting that composition is heterogeneous (Appendix 1). Four species dominate the stands in terms of cover (≥5% mean cover), including *Andropogon scoparius*, *A. gerardii*, *Poa compressa* and *Sorghastrum nutans* (Table 1). Twenty of 59 prevalent species are prevalent only in this type (Appendix 1). This is the highest percent of distinct prevalents for any of the types.

Dry-mesic prairie

Dry-mesic prairie is often found on more elevated stands in the central highlands region or near Lake Simcoe, where sandy loam soils over rocky substrate predominate. It is also found on dry sandy ridges in the Windsor and Walpole areas. Soils of the former have high organic matter (5-12%) and slightly alkaline pH (7.6), whereas the latter have lower organic matter levels (3-6%) and moderately acidic pH (5.8). Four of the 10 stands occur along railway right-of-ways.

Sixteen species have greater than 75% presence, which suggests that dry-mesic prairie composition is less variable than dry prairie. The most prevalent are *Solidago nemoralis*, *Monarda fistulosa*, *Fragaria virginiana* and *Andropogon scoparius*. Dominant species, using cover, include *Andropogon scoparius*, *A. gerardii*, *Solidago juncea*, *Hieracium florentinum*, *Carex pensylvanica*, *Aster azureus*, and *Poa compressa* (Table 1).

Eight of 68 prevalent species were restricted in prevalence to the dry-mesic prairies (Appendix 1). Weedy introduced species occur most often in these prairies, totalling 12 of the 68 prevalents.

Mesic sandy loam prairie

These stands are virtually restricted to the Windsor and Walpole areas, where they occur on sandy to sandy loam soils. Topography is fairly level, soil pH is variable, and organic matter is similar to dry-mesic stands (4-12%). Depth of A horizon is greater than in the drier prairies. Stands on Walpole had evidence of recent fires, whereas those at Windsor did not.

Table 3. Summary of environmental factors of the 40 stands along the moisture-substrate gradient. Mean values are given with ± 1 SD. Nutrient analyses for magnesium were limited to values below 200 ppm and for calcium to 2000 ppm (see Methods). Where samples exceeded these limits, mean values are given without a SD, and means represent minimum values for these segments.

Environmental	Moisture Segment					
Factor	Dry	Dry-mesic	Mesic	Wet-mesic		Wet
				sandy	sandy loam	
% sand of B horizon	85.0 ± 16.0	67.0 ± 32.0	77.0 ± 16.0	88.0 ± 6.0	57.0 ± 17.0	62.0 ± 21.0
depth of A horizon (cm)	17.0 ± 5.0	20.0 ± 9.0	32.0 ± 9.0	34.0 ± 9.0	32.0 ± 6.0	39.0 ± 7.0
organic matter of A (%)	5.6 ± 3.1	6.1 ± 4.6	7.5 ± 3.3	10.9 ± 4.2	8.8 ± 2.8	11.2 ± 2.7
pH of A horizon	6.6 ± 1.1	7.2 ± 1.1	7.1 ± 1.1	6.8 ± 1.0	7.7 ± 0.5	7.1 ± 0.9
soil water retaining cap.	55.0 ± 12.0	63.0 ± 22.0	65.0 ± 12.0	78.0 ± 9.0	80.0 ± 20.0	79.0 ± 13.0
nutrients in A horizon						
nitrogen (%)	0.4 ± 0.4	1.1*	1.9 ± 0.7	1.4 ± 0.3	1.9*	2.1 ± 0.5
phosphorus (ppm)	16.0 ± 24.0	3.0 ± 1.0	3.0 ± 1.4	4.0 ± 0.9	4.0 ± 1.5	4.0 ± 1.2
potassium (ppm)	36.0 ± 15.0	61.0 ± 17.0	37.0 ± 14.0	58.0 ± 42.0	38.0 ± 10.0	49.0 ± 19.0
magnesium (ppm)	72.0 ± 42.0	120.0	134.0	178.0	199.0	187.0
calcium (ppm)	1094.0	1568.0	1625.0	1875.0	1996.0	1933.0
fire index	1.5 ± 0.4	1.8 ± 1.3	2.8 ± 1.6	2.8 ± 1.0	4.1 ± 0.6	3.5 ± 0.3
stoniness index	1.1 ± 1.3	2.9 ± 1.8	0.0	0.2 ± 0.6	0.0	0.0
No. of stands	11	5	6	7	7	4

* no replicates

Eight of 79 prevalent species were restricted to this type (Appendix 1). Only 4 weedy introduced species are prevalent.

Wet-mesic prairies

Wet-mesic prairies are virtually restricted to the Windsor and Walpole areas where they occur on level sandy to sandy loam soils. The water table is close to the surface, but flooding is rarely evident (Hoffman 1975, Anonymous 1979). All stands have a high organic matter (6-14%), but stands at Windsor and Sarnia have a much higher percent sand content than stands at Walpole (Table 3). These substrate differences are reflected in compositional differences (Figure 3); thus two subtypes are distinguished: wet-mesic sandy prairies and wet-mesic sandy loam prairies (note, however that for purposes of standardization with other Ontario vegetation studies and for comparison with other regions, the prevalent species list for wet-mesic prairie in Appendix 1 is retained as one type).

Wet-mesic sandy prairies

These stands have a high water table for most of the year, but because of the sandy soil, temporary droughts can occur in summer (Pratt 1979). Windsor stands are moderately to slightly acidic (pH 5.6-7.4); Sarnia stands are slightly alkaline (pH 7.8-8.0). Evidence of fire was slight at time of sampling, but Windsor stands are now under a burn management programme (Pratt personal communications).

Composition of these prairies was very homogeneous, with 33 species having >75% presence. Dominants (≥5% cover) are *Calamagrostis canadensis*, *Solidago canadensis*, *Andropogon gerardii*, *Spartina pectinata*, *Pycnanthemum virginianum*, and *Rubus flagellaris*. Thirteen prevalent species were restricted to this type, including *Agrimonia parviflora*, *Celastrum scandens*, *Cicuta maculata*, *Cirsium vulgare*, *Fraxinus pensylvanica* seedlings, *Osmunda regalis*, *Onoclea sensibilis*, *Oxypolis rigidior*, *Parthenocissus inserta*, *Senecio pauperculus*, *Sisyrinchium albidum*, *Solidago rugosa*, and *Thalictrum revolutum*.

Wet-mesic sandy loam prairie

These stands, which are part of the most extensive prairie sites in Ontario, virtually occur only on the level sand plains of the St. Clair River delta at Walpole Island. Soil pH is

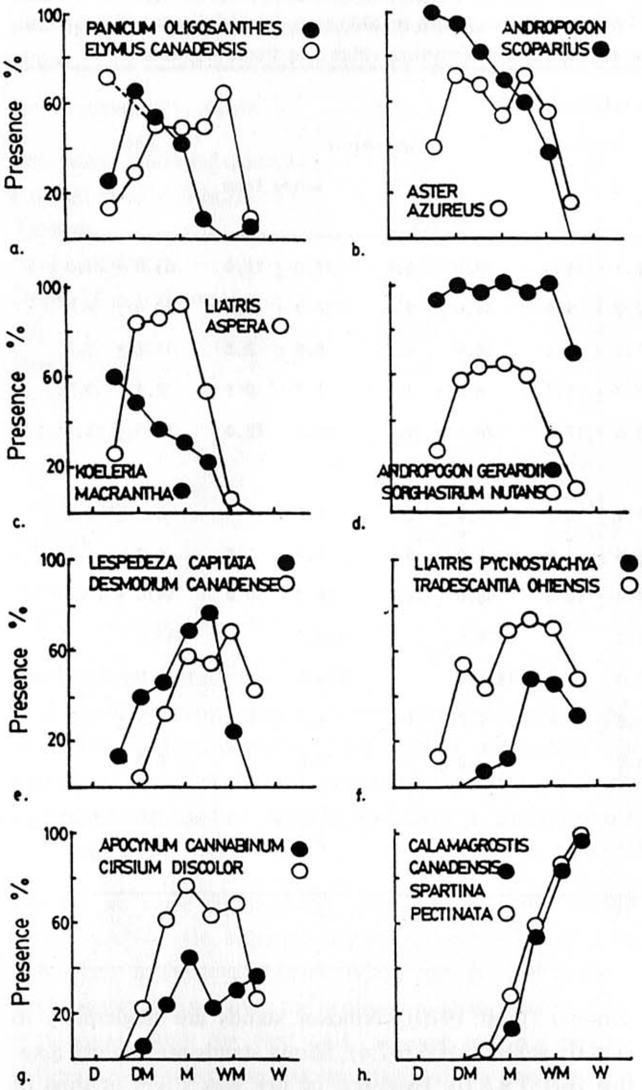

Figure 4. Species response curves along the moisture gradient for Wisconsin prairie (from Table 1, Curtis 1955). See text for explanation of dotted line in 5a.

slightly to moderately alkaline (pH 6.8-8.3). Most stands showed evidence of annual burning.

Composition was fairly homogeneous, with 24 species having a presence >75%. A number of species dominate (≥ 5% cover), including *Panicum virgatum, Andropogon gerardii, Sorghastrum nutans, Pycnanthemum virginianum, Desmodium canadense, Andropogon scoparius*, and *Fragaria virginiana*. Eleven species were prevalent only in this type, including *Aster dumosus, Carex bicknellii, Carex granularis, Erigeron philadelphicus, Erigeron pulchellus, Juncus dudleyi, Krigia biflora, Pedicularis lanceolata, Quercus palustris* seedlings, *Sisyrinchium mucronatum*, and *Tradescantia ohiensis*.

Wet prairie

These prairie stands were found only at Windsor and Walpole on level sand plains. Windsor stands were more sandy and probably less wet than those on Walpole, though both were temporarily flooded in spring. Evidence of annual fires at Walpole was high, but, because of standing water in spring, fires were also patchy.

These stands have low species richness (Table 1). Composition was very homogeneous, with 36 species having 75% presence. Dominants include *Calamagrostis canadensis, Spartina pectinata, Carex sartwellii, Aster simplex, Carex stricta*, and *Carex buxbaumii* (Table 1). Thirteen species were restricted in prevalence to this type, including *Asclepias incarnata, Carex sartwellii, Carex stricta, Carex meadii, Cirsium arvense, Galium palustre, Lythrum alatum, Mentha arvensis, Panicum boreale, Rosa blanda, Solidago ohioensis, Spirea alba*, and *Polygonum coccineum* (other apparently unique prevalents, such as *Aster umbellatus* (Appendix 1) were also prevalent in either wet-mesic sandy or sandy-loam prairies).

DISCUSSION

Composition of Ontario prairies

Prairie sites in southern Ontario contain many typical grasses and forbs of the tallgrass prairie region. Many of the characteristic plants in these prairies are rare species for Ontario (Argus and White 1977, Pratt 1979, Faber-Langendoen and Maycock 1987). Prairies in southern Ontario are most common in the southwest, especially on the Walpole Island Indian Reserve and near Windsor (Ojibway Prairie Provincial Nature Reserve), where they are associated with sand-plains.

The site-moisture gradient is useful for understanding compositional trends in prairie communities in southern Ontario. The bell-shaped response curve of many species along the direct gradient suggests that moisture, in association with other correlated factors, accounts for a significant proportion of the ecological influences (Bray 1961, Nelson and Anderson 1982). The separation of stands by DECORANA ordination, which was correlated with trends in soil moisture, supported the results of direct gradient analysis.

Ordination results also indicated several secondary compositional trends that were possibly related to environmental changes in texture and percent sand. The differences in wet-mesic sandy loam soils compared to wet-mesic sandy soils supports the use of substrate for distinguishing community types, as was done for Illinois prairies (White and Madany 1981). A recent reanalysis of Curtis' data by Umbanhower (1993) also indicated that substrate was a significant influence on prairie composition.

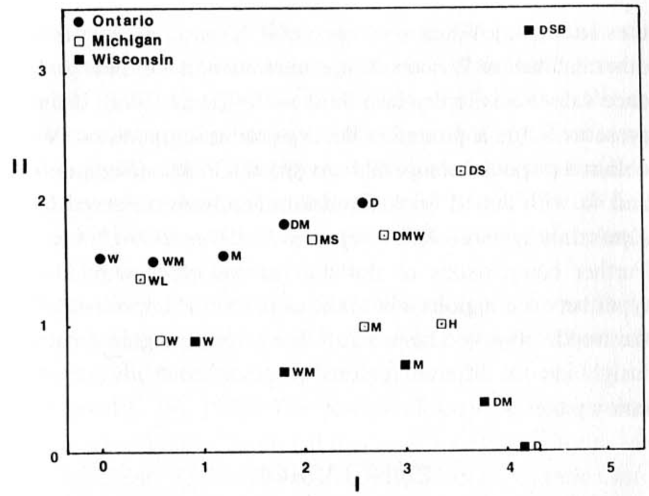

Figure 5. Detrended correspondence analysis of 18 community types in Ontario, Michigan and Wisconsin. Position of the 18 types on axis 1 and axis 2 is indicated with symbols. Ontario: W = Wet prairie, WM = Wet-mesic prairie, M = Mesic prairie, DM = Dry-mesic prairie, D = Dry prairie. Michigan: W = Wet prairie, WL = Lakeplain wet prairie, M = Mesic prairie, MS = Mesic sand prairie, DMW = Woodland prairie (dry-mesic), H = Hill prairie, DS = Dry sand prairie. Wisconsin: W = Wet prairie, WM = Wet-mesic prairie, M = Mesic prairie, DM = Dry-mesic prairie, D = Dry prairie, and DSB = Sand barrens (dry).

Plant composition of the wet-mesic loam prairies on Walpole Island differs from that of wet-mesic sand prairies at Windsor and Sarnia, particularly in the abundance of *Aster dumosus*, *Carex meadii*, *Panicum virgatum*, *Juncus balticus*, *Viola papilionacea* and *Liatris spicata* on the former. Differences between the two regions cannot be attributed solely to substrate because the fire index values for Walpole were much higher. This may account for the greater abundance of species such as *Rubus flagellaris* at Windsor.

Heterogeneity in species composition between stands increased with increasing dryness (Figure 2). Drier prairie sites are geographically more widespread throughout southern Ontario, and are quite distinct in composition from wetter prairies in the Windsor and Walpole area (Figure 2). The location of dry sites in a variety of habitats, whether inland dune systems, glacial beach shorelines, or rocky slopes indicates the unusual features needed to maintain these communities. In addition, their location along railway rights of way, and even Indian trails (Reznicek 1983) suggest that some cultural practices, whether clearing or fires, may also have maintained the open character of these sites.

Fire frequency usually increases with increasing dryness (up to a point), but the reverse trends observed here are primarily a reflection of cultural practices by residents on Walpole Island Indian Reserve, who burn many of the wetter sites almost annually. Without fire wetter sites may undergo more rapid succession to wet savanna or forest (Curtis 1959, Schroeder 1982). The importance of fire in preventing succession was observed at Ojibway Prairie Provincial Nature Reserve, where, prior to the introduction of a fire management system, prairie was succeeding to savanna and wet-mesic forest. Rates of succession in wet versus dry prairie are virtually unknown, but wetter savannas have been observed to succeed to forest more rapidly than dry (Abrams 1986).

The greater number of introduced or weedy dominants in drier compared to wetter prairies suggests that lack of fire may be affecting their composition. Fire selects against many introduced species (Henderson 1982) and favours prairie grasses (Abrams, Knapp and Hulbert 1986). Loucks et al. (1985) suggested that drier sand prairies were structurally more open and thus vulnerable to invasion, an observation also made in Iowa sand prairie (White and Glenn-Lewin 1984). The small size of Ontario sites (often less than 0.5 ha) and their location closer to agricultural fields may also increase their vulnerability.

Comparisons with other prairie regions

Comparisons of Ontario prairie to those of Michigan and Wisconsin prairie and prairie-related communities are presented in Figure 5. Wet and wet-mesic prairie in southern Ontario were most similar to lakeplain wet prairies in Michigan. Michigan's wet prairies are similar to wet and wet-mesic prairies in Wisconsin. Ontario mesic and dry-mesic prairies were most similar to Michigan mesic sand prairie. Michigan and Wisconsin mesic prairies were quite similar. Finally, Ontario dry prairie was most similar to Michigan's woodland prairie. Wisconsin dry and dry-mesic prairies were strongly separated on the second axis from Michigan and Ontario dry prairies, which showed more similarity to the dry sand prairies and barrens.

When comparing Ontario prairie to prairie-related communities in Wisconsin, the Ontario dry-mesic and dry prairie had a higher index of similarity to Wisconsin oak barrens (37%) and oak openings (38%) than to any of Wisconsin's dry to mesic prairies (24-33%). Overall the wetter Ontario prairies had greatest similarities to Wisconsin and Michigan wet prairies, whereas drier Ontario prairies showed greatest similarities to dry sand prairies and oak savannas.

Species which are prevalent in Ontario prairie and not commonly associated with those further west include *Agrimonia parviflora*, *Aster dumosus*, *Celastrus scandens*, *Gerardia tenuifolia*, *Helianthus giganteus*, *Juncus greenei*, *J. tenuis*, *Luzula multiflora*, *Panicum lanuginosum* var. *implicatum*, *Parthenocissus inserta*, *Scleria triglomerata*, *Solidago rugosa*, and *Vernonia altissima* (Appendix 1).

Species in Ontario dry prairie that are typically found in Wisconsin savannas (the "modal species" of Curtis) include *Antennaria neglecta*, *Comandra richardsiana*, *Euphorbia corollata*, *Helianthemum canadense*, *Krigia biflora*, *Lespedeza capitata*, *Lithospermum canescens*, *Lupinus perennis*, *Panicum praecocius*, *Physalis virginiana*, *Tephrosia virginiana*, and *Viola sagitta*. These species can occur as drier prairie associates, but they are most typical of savannas in the prairie-forest border (Curtis 1959). This may be a feature of tallgrass prairie at its northeastern limits. However, whereas Ontario wet prairies contain all of the grass dominants of wet prairies further west, Ontario dry prairie are often missing several significant species, including *Bouteloua curtipendula* and *Sporobolus heterolepis* of drier loam prairie in Illinois (White and Madany 1981), and *Panicum perlongum*, *Stipa spartea* and *Koeleria macrantha* in Wisconsin.

We can also compare the environmental gradient response of species in Wisconsin prairie (Figure 4) to those in Ontario (Figure 1). Wisconsin data have more intermediate points because Curtis (1955) used weighted species scores to indirectly indicate the moisture status of a stand. These graphs show a strong degree of similarity, not only in terms of the shapes of the curves, but in levels of presence. Species appear to be responding in very similar fashion to comparable moisture influences. Even those species in Ontario prairies that show bimodal trends are seen to respond similarly in Wisconsin. *Liatris spicata* occurs rarely in Wisconsin but is similar taxonomically to *Liatris pycnostachya*, which is not found in Ontario. The two species have a very similar ecological response along the gradient (Figures 1f and 4f).

There are some notable differences in species response between the two regions in the drier stands, where *Panicum oligosanthes* and *Elymus canadensis* have higher presence values in Ontario's dry stands (Figures 1a and 4a) and *Liatris aspera* and *Koeleria macrantha* have higher values in the dry-mesic (Figures 1c and 4c). The species that differs most between these regions is *Elymus canadensis*. It is most constant in dry prairies of Ontario but is optimal in wet-mesic prairies of Wisconsin.

Ontario dry prairies also differ from those in Wisconsin in terms of physiography. Ontario sites are primarily ancient inland stabilized dune systems and glacial beach shorelines, with some stony slopes, but in Wisconsin dry prairie occurs almost exclusively on inland steep hillsides with thin soil. This in turn affects their species composition. For example, *Elymus canadensis* was seen to differ substantially in species response between Wisconsin and Ontario dry prairies (Figures 1a and 4a). When the response of *Elymus canadensis* in other habitats in Wisconsin was examined, its highest presence values was in dry lake dune sites (Curtis 1959). If this presence value is plotted in the dry prairie segment then we obtain a response comparable to that in Ontario (Figures 1a and 4a with dotted line). Similar trends were observed for *Equisetum hyemale*, *Poa compressa*, and *Oenothera biennis*. Further comparisons of floristic lists of other vegetation types between regions will allow us to test the importance of the trends observed here. In so doing we may gain greater insight into the different regional processes controlling vegetation patterns.

CONCLUSION

In conclusion, prairies in southern Ontario are favoured by a unique combination of moisture, sandy and stony substrates, and frequent fires. Many sites show a striking resemblance to prairie sites farther west in the prairie-forest border and have persisted in the region for many hundreds of years. Drier sites on inland stabilized sand dunes and glacial beach shorelines continue to support a number of prairie and prairie-like communities, but have a variable composition that is less related to drier prairies farther west. These areas show high resemblance to sand prairies and oak savanna. Together these prairies and associated communities comprise a distinctive grassland vegetation type within southern Ontario's deciduous forest region.

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Appendix 1. List of prevalent species for the five moisture segments of Ontario prairie. Species are arranged alphabetically with their % presence within a segment. Absence of a value indicates the species was not prevalent in the segment, but it may have been present at some lower value.

	Moisture Segment (No. of Stands)				
Species	Dry (19)	Dry-mesic (10)	Mesic (9)	Wet-mesic (19)	Wet (6)
Achillea millefolium		60	67		
Agropyron repens	68				
Agrostis gigantea		70	100	68	50
Andropogon gerardii	89	90	89	89	50
Andropogon scoparius	95	90	67	47	
Anemone cylindrica	74	70	67		
Anemone virginiana		40			
Antennaria neglecta	42	70	67		
Antennaria plantaginifolia	42				
Apios americana		40	44	63	
Apocynum androsaemifolium	47				
Apocynum cannabinum		40	89	84	100
Arenaria stricta	42				
Aristida purpurascens			44		
Asclepias incarnata					50
Asclepias sullivantii			44		50
Asclepias syriaca	53				
Asclepias tuberosa	63	40	56		
Asparagus officinale			56		
Aster azureus	68	90	89	58	
Aster dumosus				42	
Aster ericoides	42	80	100	84	67
Aster laevis	37	40	56		
Aster novae-angliae		50	78	84	100
Aster sagittifolius	30				
Aster simplex			56	58	100
Aster umbellatus					34
Calamagrostis canadensis		30	67	95	100
Carex bicknellii				37	
Carex buxbaumii				37	100
Carex conoidea					50
Carex granularis				37	
Carex lanuginosa			44	58	83
Carex muhlenbergii	32				
Carex pensylvanica	42	80	78		
Carex sartwellii					67
Carex stricta					67
Ceanothus americanus	37				
Cerastium vulgatum		40			
Chrysanthemum leucanthemum		40			
Cicuta maculata				42	
Cirsium arvense					50

Appendix 1, continued.

Cirsium discolor		40	67	42	83
Comandra richardsiana	47	50	56	53	
Convolvulus sepium			56	37	83
Coreopsis tripteris			56		
Cornus obliqua					50
Cornus racemosa	37	80	89	74	83
Corylus americanus			44		
Cyperus filiculmis	42				
Danthonia spicata	37	50			
Daucus carota	58	60	56		50
Desmodium canadense	47	80	100	89	67
Dryopteris palustris				63	83
Eleocharis elliptica			44	58	83
Elymus canadensis	37				
Equisetum arvense	37	50	78	84	
Equisetum hyemale	42	40	67		
Erigeron canadensis	32				
Erigeron philadelphicus				37	
Erigeron strigosus		50	56		
Eupatorium maculatum					50
Euphorbia corollata	37	40	44		
Fragaria virginiana	58	100	89	84	67
Galium boreale	42				
Galium palustre					50
Geranium maculatum		40			
Gerardia purpurea			44	37	67
Gerardia tenuifolia				37	
Helenium autumnale			44	58	100
Helianthemum canadense	32				
Helianthus giganteus				68	100
Hieracium florentinum	42	40			
Hypericum perforatum	63	50			
Hypoxis hirsuta			44	63	83
Iris versicolor				37	100
Juncus balticus		30	33	53	
Juncus dudleyi				37	
Juncus greenei			56		
Juncus tenuis			67		
Juncus torreyi				58	
Krigia biflora				37	
Lathyrus palustris			44	74	100
Lechea intermedia	32				
Lespedeza capitata	68	70	78		
Liatris aspera		40			
Liatris cylindracea	47				
Liatris spicata		40	89	74	50
Linaria vulgaris	37	40			
Lithospermum canescens		40			
Lobelia spicata			67	47	
Luzula multiflora			44		
Lycopus americanus			56	63	83

Appendix 1, continued.

Lycopus uniflorus				42	83
Lysimachia quadriflora			56	68	83
Lythrum alatum					67
Melilotus alba	63	60	33		
Mentha arvensis					50
Monarda fistulosa	63	100	100	79	34
Muhlenbergia mexicana			56	42	
Oenothera biennis	58	50		42	
Onoclea sensibilis				37	
Panicum boreale					34
Panicum lan. var implicatum		50	33	47	34
Panicum oligosanthes	42				
Panicum sphaerocarpon			44		
Panicum virgatum		30	100	79	67
Pedicularis lanceolata				37	
Plantago lanceolata		30			
Poa compressa	84	90	78		
Poa pratensis	84	80	89	68	67
Polygala sanguinea		40			
Polygonum coccineum					67
Populus deltoides (sdlgs)			44		
Potentilla recta	47	30			
Potentilla simplex	32		44		34
Prenanthes racemosa				53	
Prunella vulgaris		60	67		
Prunus virginiana	47	40			
Pteridium aquilinum	37				
Pycnanthemum virginianum		40	89	84	83
Pyrus malus (sdlgs)		40			
Quercus palustris (sdlgs)				42	
Quercus velutina (sdlgs)	58	40			
Rhus aromatica	47				
Rhus glabra			56		
Rhus radicans	58				
Rhus typhina	74	40			
Rosa blanda					67
Rubus flagellaris					34
Rudbeckia serotina		80	100	89	83
Rumex acetosella	47				
Salix discolor				37	
Salix humilis		60	56	37	
Scleria triglomerata			67		
Senecio aureus				42	34
Solidago altissima		50	67	42	34
Solidago canadensis	63	80	78	68	100
Solidago gigantea			56	68	34
Solidago graminifolia		60	100	74	100
Solidago juncea	74	90	56	37	50
Solidago nemoralis	84	100	67		
Solidago ohioensis					34
Solidago riddellii			44	37	

Appendix 1, continued.

Solidago rigida		40	78	53	
Sorghastrum nutans	53	80	78	74	67
Spartina pectinata			56	74	100
Spirea alba					50
Sporobolus asper			33		
Sporobolus cryptandrus	37				
Taraxacum officinale		30			
Thalictrum polygamum				42	
Tragopogon pratensis	53				
Verbascum thapsus	58				
Vernonia altissima			78	79	83
Veronica officinalis		30			
Veronicastrum virginicum		40	89	79	50
Viola papilionacea			33	47	50
Vitis riparia	68	70	89	84	50
Zizea aurea			33	42	
No. of prevalents (= avg. no. of species per stand)	59	68	79	72	63
Total species	212	234	205	238	147
No. of stands	19	10	9	19	6