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The alvars of the Maxton Plains, Drummond Island, Michigan: Present Community Composition and Vegetation Changes.

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THE ALVARS OF THE MAXTON PLAINS, DRUMMOND ISLAND, MICHIGAN: PRESENT COMMUNITY COMPOSITION AND VEGETATION CHANGES

By

Patrick Stephen Herendeen

A THESIS

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ABSTRACT

THE ALVARS OF THE MAXTON PLAINS,
DRUMMOND ISLAND, MICHIGAN:
PRESENT COMMUNITY COMPOSITION AND VEGETATION CHANGES

By

Patrick Stephen Herendeen

The alvar vegetation of the Maxton Plains, Drummond Island, Michigan is examined. Alvars are defined as areas of horizontal limestone or dolomite with shallow soil, supporting an open vegetation dominated by herbaceous plants. On the Maxton Plains these communities are largely dominated by members of the Poaceae and Cyperaceae. The alvars of the Maxton Plains are compared with the alvars in Ontario, Canada and Oland, Sweden. Similarities in the physical setting and vegetation between these regions are discussed. Through plot sampling in eleven alvar sites, composition of the Maxton Plains alvars and its variability is studied. Similarity of sites is calculated using Horn's index.

Aspects of the history of the alvar vegetation are examined through use of aerial photographs and deposits of opal phytoliths in the soils. Differences between the aerial photographs taken in 1939 and 1977 indicate some areas of change in position of the alvar-forest boundary. Opal phytolith deposits provide evidence that is interpreted to suggest an oscillation of the forest-alvar boundary.

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INTRODUCTION

This study of the alvars of the Maxton Plains of Drummond Island was initiated for several reasons. Very little has been published concerning this area and it is hoped that this study will contribute some information in this regard. The physical setting of the region and the vegetation are quite unusual. The alvars are areas of horizontally bedded dolomite with very shallow soil and they support a vegetation dominated by grasses, sedges and other herbaceous taxa. The occurrence of a grassland community in northern Michigan is unexpected. The composition of these grasslands is unusual in that they are composed of a large number of both midcontinental and northern disjunct species. There are nine vascular plant species occurring on the alvars that are listed as either "threatened" or of "special concern" in Michigan. These grasslands are also unique in that they are the only areas in Michigan that are dominated by three state listed taxa, namely: Sporobolus heterolepis, Eleocharis compressa and Carex scirpoidea.

The objectives of this study are as follows:

1) To evaluate the composition of the alvar vegetation, as well as its variability between sites.
2) To evaluate similarities between sites.

3) To investigate relationships between biogeographic groups of species.
4) To investigate relationships of species composition to size of alvar site.
5) To study aspects of the history of the alvar vegetation.

The vegetation analysis is based on plot sampling in eleven sites and species lists for 18 other alvar sites. Study of the vegetation history is based on use of aerial photographs from 1939 and 1977, as well as on analysis of opal phytolith deposits in the soils of the alvars and adjacent transitional areas.

With few exceptions nomenclature for plant species follows Voss (1972) for the Gymnosperms and Monocots and Gleason and Cronquist (1963) for the Dicots. Voucher specimens are deposited in the Michigan State University Herbarium (MSC).

This report will start with a summary of the geological setting of the study area and a summary of the postglacial vegetation history and climate of the Great Lakes region. Comparisons of the Maxton Plains alvars will then be made with the alvars of both Ontario and Oland, Sweden. These comparisons will make clear the unusual nature of alvar regions. The vegetation analysis will follow and the report will then conclude with the investigation of vegetation changes.

GEOLOGICAL SETTING.

Geology of Drummond Island.

The bedrock of Drummond Island is composed of dolomite of the Niagaran Series (Middle Silurian). This unit is part of a broadly curving arc of resistant rock which extends from Niagara Falls, north through the Bruce Peninsula, north and west to the islands of Lake Huron, west to the southern part of the Upper Peninsula of Michigan and then south to the Door Peninsula of Wisconsin. On much of northern Drummond Island the overlying Devonian shales and limestones have been eroded away to expose a flat, shallowly dipping dolomite "pavement" (Dorr and Eschman, 1970).

The bedrock surface on the plains is nearly flat to slightly rolling and slopes from northwest to southeast with a gradient of one percent or less. A series of ledges runs roughly east-west across the western part of the Maxton Plains and vary in height from one to two meters. These ledges could be old shoreline features or they could be the result of glacial plucking.

Areas just north of a ledge tend to be quite wet and poorly drained due to the damming effect of the ledges while those areas immediatly south of a ledge tend to be much drier. Vegetation zones tend to conform to these physical features quite closely.

The dolomite exhibits a jointing pattern which is quite conspicuous over large areas of the Maxton Plains. Joints in the dolomite serve to trap weathered rock and fine grained mineral matter, organic materials and water which may then promote colonization by plants. These vertical joints provide a source of moisture to the immediately adjacent vegetation, even through the driest periods. An equivalent amount of water is unavailable to plants located only a short distance away.

The southern portion (approximatly half) of Drummond Island is covered by surface deposits of lake sediment origin while the northern portion is reported to have surface deposits originating from glacial end moraines. However, over an extensive portion of the Maxton Plains there is little or no glacial till, though there are many glacial erratic boulders scattered throughout. It has not been determined whether till was never deposited in these areas or that it was originally present but was later removed through water erosion during fluctuating postglacial lake levels.

As a result of this scanty deposit, all mineral material for soil development must have either come from the products of dolomite weathering or have been transported in by air or water. Much of the silicate clay and fine sand in the scanty soils are likely derived from the dolomite parent material since silica constitutes approximately five percent (by weight) of this rock.

Late Quaternary history of lake levels.

At the peak of the Wisconsinan glaciation, all of Michigan was covered by glacial ice. The deglaciation process involved several temporary retreats and readvances of the ice. Final deglaciation of eastern upper Michigan began after the peak of the Greatlakean ice advance about 11,500y B.P.(years before present). As the ice retreated, Lake Algonquin expanded northward. The first halt in deglaciation of the Upper Peninsula is marked by the Newberry Moraine. A second, longer lasting halt is represented by the Munising Moraine where the ice front remained for perhaps several centuries, allowing development of the main Lake Algonquin strandlines (Futyma, 1981).

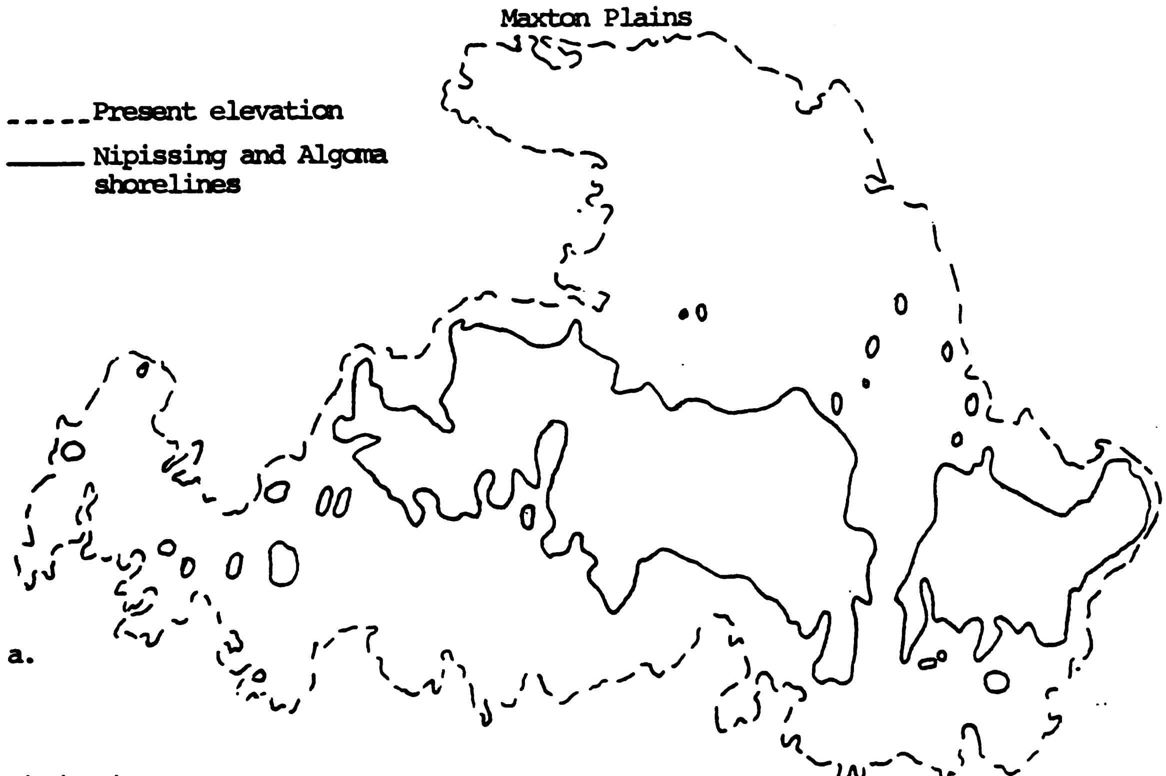
At the maximum extent of Lake Algonquin (ca. 10,600y B.P.) most of eastern upper Michigan, all of Drummond Island and most of Manitoulin Island were under water. Most of the exposed land of this region consisted of small islands, mostly on the Newberry Moraine and the Niagara escarpment. The outlets of Lake Algonquin are placed at 605 ft at the DesPlaines and St. Clair Rivers (Flint, 1971). Due to differential rebound the strandlines that mark the Algonquin level in northern Michigan are considerably higher. The isobase trend (lines of equal deformation) was determined by Futyma (1981) to be S. 75^{o} E. Though Futyma did not specificly examine Drummond Island, the maximum Algonquin lake surface can be estimated from the isobase trend to have been roughly 919 ft. (280 m) for this area. There was no exposed land on Drummond Island at this time since the highest point on the island is 750 ft.

In the Huron basin the main Algonquin stage ended ca. 10,600y B.P. with the opening of successively lower outlets to the east through North Bay. The water level continued to drop to a low water phase (Lake Stanley- Huron basin, Lake Chippewa- Michigan basin), which was reached by ca. 9800y B.P. (Terasmae and Hughes, 1960; Hough, 1963; Wayne and Zumberge, 1965). According to Flint (1971), the outlet for Lake Stanley was the Ottawa River at 165 ft. (present elevation) and the Lake Chippewa outlet was the Mackinac River at 230 ft. Hough (1963) estimated the original elevation of Lake Stanley to have been 180-200 ft.

The Lake Stanley-Chippewa phase ended with elevation of the North Bay outlet. Water levels rose for approximately 3,000 - 4,000 years until discharge was resumed through the stable Algonquin outlets at Chicago (Des Plaines River) and Port Huron (St. Clair River), in addition to the outlet at North Bay. This triple outlet phase defines the Nipissing Great Lakes phase in postglacial lake level fluctuations and is now thought to have occurred from ca. 6,100 to 3,900y B.P. with a peak water level of 605 ft. at the outlet, dated at ca. 5,500y B.P. (Lewis, 1968; Smith, 1968; Harrison, 1971). Nipissing strandlines are well developed erosional features in northern Lake Huron. The shoreline at Sault Ste. Marie is represented by a 9 - 15 meter bluff with its base at about 197 m. (645 - 650 ft.) (Cowan, 1978). Lewis (1970) reports Nipissing shoreline features on Manitoulin Island to range from 640 ft. (195 m.) on the south to 655 ft. (200 m.) on the north end of the island. Prominent bluffs south of the Maxton Plains on Drummond Island are within the range of elevations reported above and are likely Nipissing in origin. Figure 1a shows the extent of exposed land on Drummond Island during the stable phase of Lake Nipissing. At this time all of the Maxton Plains was under water.

The Nipissing Great Lakes phase ends with the closing of the North Bay outlet through the Ottawa River and the gradual lowering of water level by erosion of the Des Plaines River and St. Clair River outlets. The water level dropped for approximately 500 years until it reached a temporarily stable level at 592 ft. (180 m.) by about 3,200y B.P. Water level was maintained during the Algoma phase, 3,200y B.P. to ca. 2,500y B.P. (Lewis, 1970). Elevations of Algoma strandlines near Little Current, Manitoulin Island are suggested to be ca. 625 ft. (190.5m) (Lewis, 1968). Figure 1b illustrates the approximate position of the Algoma shorelines on the Maxton Plains of Drummond Island. Renewed erosion of the Port Huron outlet allowed gradual lowering of water level to reach 580 ft. (176.8 m) (based on present elevation) by ca. 2,000y B.P. (Wayne and Zumberge, 1965).

Time of emergence of a land area such as the Maxton Plains from Lake Huron can be estimated from the timing of lake level changes and the rate of rebound. Lewis (1970)



Nipissing

Algoma

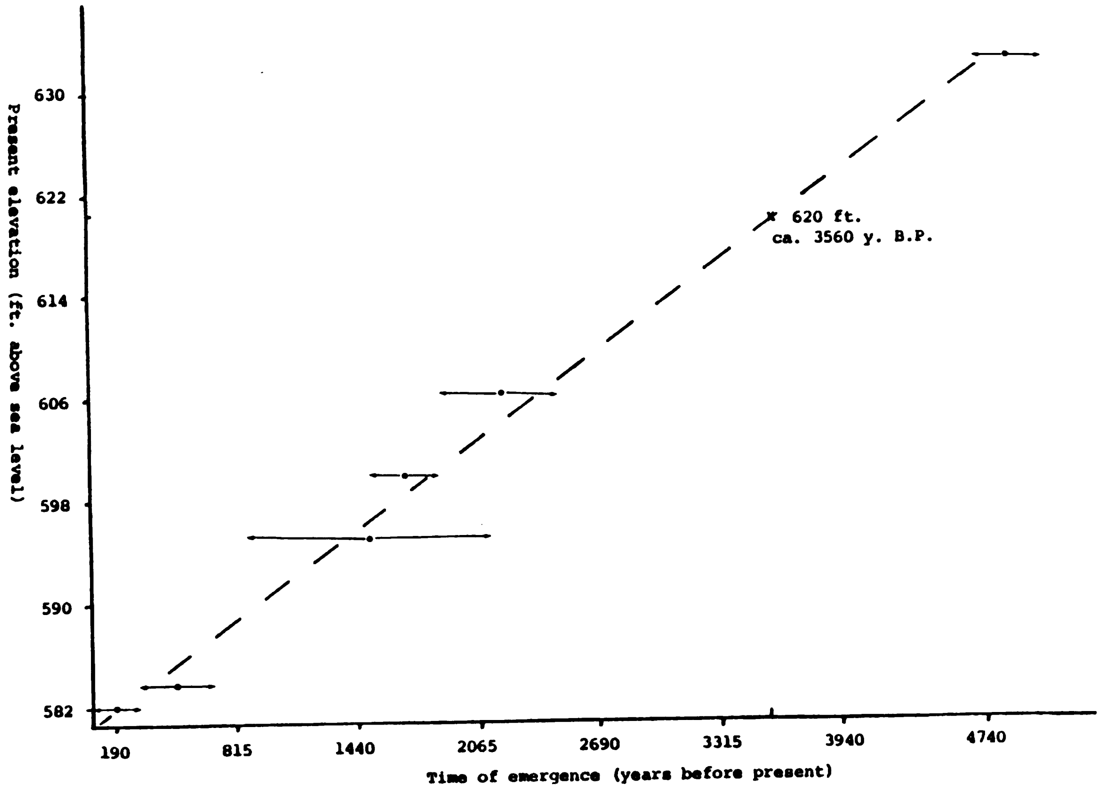
Figure 1 Approximate shorelines (present elevation) for the Nipissing (ca. 650 ft.) and Algoma (ca. 625 ft.) Great Lakes stages.

made the following measurements and calculations for recent uplift on Manitoulin Island. The total amount of post Nipissing emergence above Lake Huron is 18-23 m. (60-75 ft.): 6.7 m. (22 ft.) by lowering of lake level and the remainder, 11.3-16.3 m. (38-53 ft.), is due to uplift. Lewis calculates the uplift to have been at a constant rate of 2.2±.7 mm/yr. (0.73±.2 ft/100yrs.) for the past 5,000 years for Little Current, Manitoulin Island. Lewis has identified and dated old shoreline features and organic deposits on Manitoulin Island and relates their present elevation to elevation at the time of emergence from Lake Huron. The followingis a partial listing of these sites showing present elevation, original elevation and time of emergence:

Present Elevation	Original Site Elevation	Time of Emergence
582.0ft.(177.4m.)	581.0ft.(177.1m.)	190±130yBP
584.0ft.(178.0m.)	582.3ft.(177.5m.)	510±180yBP
595.1ft.(181.4m.)	587.3ft.(179.0m.)	1500±600yBP
600.0ft.(182.9m.)	587.9ft.(179.2m.)	1660±150yBP
606.6ft.(185.0m.)	590.2ft.(179.9m.)	2180±300yBP
632.2ft.(192.7m.)	602.4ft.(183.6m.)	4740±140yBP

Assuming that the rates of rebound on Drummond and Manitoulin Islands have not been significantly different, it is possible to estimate time of emergence of the Maxton Plains area from these data. Figure 2 represents the elevations of these dated shoreline features plotted against time of emergence. From these data it is possible to correlate these variables and predict time of emergence for

Figure 2 Time of emergence of land from the waters of Lake Huron. Data represent radio carbon dated shoreline features from Manitoulin Island. The shoreline of Lake Huron is calculated to have been at the 620 ft level (present elevation) approximately 3560 years ago. Data is from Lewis (1970).



Present elevation (ft. above sea level)
630
622
614
606
598
590
582
x 620 ft.
ca. 3560 y. B.P.
190
815
1440
2065
2690
3315
3940
4740
Time of emergence (years before present)

Figure 2.

a given elevation. The 620 ft. level on Manitoulin Island is predicted to have first been exposed ca. 3558 years ago. It is evident from this information that the main part of the Maxton Plains (590-615 ft.) has been above water and available for plant growth for less than 3,500 years. It should be noted, however, that this time represents the time of final emergence from the water and that there have been areas of continually exposed and chronically disturbed land available, fluctuating shorelines and isolated high points, for colonization by plants since the decline of Lake Algonquin water levels.

SUMMARY OF THE POSTGLACIAL VEGETATION HISTORY AND CLIMATE OF THE GREAT LAKES REGION.

Introduction.

The sequence of postglacial vegetation and climatic changes in the Great Lakes region are reviewed briefly here so that the characteristics of the present vegetation of the Maxton Plains can be understood and compared with the vegetation of the surrounding region and put into a historical context. The pertinent literature is too voluminous to review thoroughly but several comprehensive reviews are available (Ogden, 1969; Davis,1983 and Webb *et al*., 1983). There have been few palynological studies reported from the northwest end of the Lake Huron basin. Recently palynological studies in eastern Upper Michigan (Futyma, 1982) and on Manitoulin Island (Warner, 1980) have been reported. Most of the studies which concern regional vegetation history and climate change have been conducted on sites in Minnesota, Wisconsin, northern Illinois and Indiana and southern Michigan. It would be helpful to have more palynological evidence from along the shores of the Great Lakes so that migrations associated with these shorelines could be better assessed. Unfortunately studies from these areas are also limited in number. An outline of the timing and nature of the major vegetation changes and migration routes is given in the following paragraphs and then evidence for prairie expansion and for Holocene climatic changes is considered in more detail.

General vegetation history.

The late-glacial vegetation record in the Great Lakes region provides evidence of a short-lived, narrow belt of tundra, whereas in southern New England there is evidence for a much longer interval of tundra vegetation, lasting perhaps until 12,000 y. B.P. (Davis, 1967). Terasmae (1967) notes that there is no evidence of a long-lasting tundra environment anywhere north of the Great Lakes in late-glacial time. He also shows that as northern Lake Superior was being deglaciated about 10,000 y. B.P., arctic species could have invaded the northern Great Lakes region by several routes, all restricted to lakeshore and riverside habitats. These are: 1) west of Lake Superior, 2) at Sault Ste. Marie through the Upper Peninsula of Michigan, and 3) through southern Ontario by way of the Bruce Peninsula and around Georgian Bay. Arctic species had migrated into the northern Great Lakes region by 9,000 y. B.P.

Tundra vegetation was very rapidly invaded byelements of the early boreal forest assemblage, being replaced in all but the most sheltered areas along the lakes (Terasmae 1967). One such protected area still supporting species with tundra affinities was described from the Old Woman Bay of Lake Superior by Soper and Maycock (1963).

Warner (1980) concludes that the first vegetation to colonize the bedrock highlands of Manitoulin Island approximately 10,500 y. B.P. was probably an open, prairie-like, spruce parkland, dominated by grasses and sedges. He considers that this vegetation probably resembled the vegetation that covers Great Coche Island today, a region that is quite similar to the Maxton Plains.

The exact nature and extent of the early boreal forest is still in question because of several unusual characteristics of the pollen record. Terasmae (1968) believes that the late-glacial boreal forest was probably more open because of the greater percentage of nonarboreal pollen in these assemblages. Cushing (1965) notes that the pollen of spruce-dominated, boreal forest areas are unusually rich in pollen of heleophilous herbaceous taxa such as Artemisia and Ambrosia and in other species from differing biogeographic affinities. This assemblage has been interpreted in various ways including: reworked sediments; long distance transport of pollen of deciduous forest types into an open vegetation near the northern treeline; mixed coniferous hardwood forest with nearby grassland; and a mixture of vegetation types including swamp, coniferous forest, oak savanna and prairie. Cushing (1965) points out that with the diversity of microhabitats that were possible on this new landscape, such a diversity of species assemblages could be possible. Davis (1967) notes that the vegetation of the same period (ca. 12,000-10,500 y. B.P.) in New England may have resembled a park-tundra or spruce-oak woodland and that by 10,500 y. B.P. an open spruce woodland had developed.

Late-glacial time in the Great Lakes region and New England was one of continual vegetational disequilibrium resulting from climatic change, soil development and species migrations (Delcourt and Delcourt, 1983). The Delcourts note that during this time the ecotone between boreal forest and deciduous forest widened into a broad belt (latitudinal) which extended from the western Great Lakes to New England. Climatic change in eastern North America has been addressed by many, most recently by Bryson (1983), Bartlein et al. (1984) and Dean et al. (1984). Davis (1983) has presented rates and directions of Holocene migrations of boreal and deciduous forest taxa onto the deglaciated landscape of eastern North America.

By 11,000-10,000 y. B.P. the boreal forest of the Great Lakes region started to deteriorate, presumably due to climatic change but perhaps also as a result of differences in migration rates between various species (Wright, 1964, 1968a). In the area north of Lake Huron and east of Lake Superior the early boreal forest was replaced by the Great Lakes-St. Lawrence forest (=Northern Mixed Hardwood Forest) which has occupied that region ever since (Terasmae 1968). Throughout the middlewest, openings in the boreal forest created by fire and windthrow were gradually being filled by combinations of birch, alder, pine, oak and elm, depending onlocality (Wright, 1968b). This transitional forest was soon replaced (within 1,000 years) by the developing prairies in eastern and northern Minnesota (Wright, 1968a). The work of Webb *et al*. (1983) supports this timing of the development of prairie vegetation in this region.

Other views as to the sequence and timing of vegetation changes coincident with the time of decline of the early boreal forest must also be recognized. Geis and Boggess (1968) and Gleason (1922) postulated that prairie vegetation replaced boreal forest with no intervening deciduous hardwood stage. Transeau (1933) considered that the boreal forest was replaced with deciduous taxa and that prairie expansion occurred subsequent to this. Benninghoff (1964) proposed that prairie vegetation existed much earlier in late-glacial time as openings in the boreal forest and that it functioned as a barrier to the migration of certain temperate forest taxa.

The composition, floristic richness and duration of a mixed hardwood forest in the Great Lakes region was probably largely dependent on location. Wright (1968a) shows that in Illinois, boreal forest gave way to deciduous forest, whereas in Kansas and Nebraskaprairie succeeded boreal forest almost immediately. Prairie did not reach Illinois until 8,000 y B.P.

Migration routes.

Various migration routes have been suggested in discussions of vegetation development. Davis (1983) uses pollen records for boreal and deciduous forest taxa of eastern North America to examine rates and directions of movement. Her work points out the individualistic nature of species movements and the fact that vegetation did not change with one formation replacing another, but rather with individual species becoming established and others declining.

The western, southern and eastern migration routes into northern Ontario (Teresmae, 1967) have already been outlined. Terasmae also notes that the migration routes for arctic species were likely restricted to lakeshores and riverbank habitats. The levels, lateral extent and outlets of the glacial lakes changed rapidly and this could have been quite important in the dispersal of arctic and other water dispersed species. Terasmae (1968) notes that species could migrate northward on the Bruce Peninsula and then to Manitoulin Island without crossing any water barriers. When drainage from Lake Huron to the Georgian Bay shifted to the channel between Manitoulin Is. and the Bruce Peninsula, all those species that had reached Manitoulin Is. could migrate on to Cockburn Is. and Drummond Is. Similarly, migrations of taxa of other biogeographic affinities from other directions along the shorelines must have been possible.

Some forest taxa are suggested to have migrated in association with the Great Lakes. Curtis (1959) and Wright (1964) infer that pine and other taxa reached Minnesota and Wisconsin by way of the northern end of Lake Michigan. Benninghoff (1963) suggests that <u>Fagus</u> and <u>Tsuga</u> reached

Michigan from the east along the north shore of Lake Erie. Curtis (1959) notes that during the time when Lake Michigan had dwindled to the low Lake Chippewa stage (ca. 10,000-9,000 y B.P.) there was ample opportunity, with the reduced water barrier, for direct westward migration of forest taxa from lower Michigan, and, I wish to add, for direct eastward migration of prairie taxa.

The Prairie Peninsula.

The Prairie Peninsula is a continuous wedge-shaped area of grassland vegetation which extends eastward from the eastern edge of the prairie in Iowa to northern Indiana and then as isolated localities in northern and southwestern Ohio and southern Michigan. The Prairie Peninsula was originally described by Transeau (1935) in a paper outlining characteristics of the formation and the surrounding vegetation.

There has been much debate as to the timing and causes of the origin of this extension of the prairie. Much of the debate is no doubt due to the fact that the patterns of vegetation changes have been different in different geographic areas. Transeau (1935) postulated that a climatic change resulting in a greater frequency of prolonged droughts caused an expansion of prairie into the deciduous forest and that fires and exposure have since favored the persistence of the prairie vegetation. Similarly, Wright (1968a) states that, in Minnesota, the

Prairie Peninsula dates from mid-postglacial time and was due to recurrent summer droughts eliminating mesic deciduous trees, while in Kansas and Nebraska, prairie succeeded the boreal forest immediately. Geis and Boggess (1968) and King (1981) show that in Illinois the Prairie Peninsula was established by 8,000 y B.P. and that it followed the late-glacial boreal forest, prior to the invasion of deciduous hardwood taxa.

Several students have suggested that the expansion of the prairie, and associated climatic changes, were asynchronous throughout the midwest and eastern United States, both north to south and west to east. Wright (1968a) notes that the period of drier and/or warmer climatic conditions (Xerothermic or Hypsithermal) appears to have occurred earlier in central Minnesota than it did in New England. Recently a detailed chronology of these events in the midwest was assembled by Webb et al. (1983). They show several interesting features of the asynchronous movement of the prairie-forest ecotone. They show that by 9,000 y B.P. prairie forb pollen types had increased and the 10% contour (of prairie pollen in relation to total counted) had moved eastward from western Minnesota and Iowa to southwestern Wisconsin and northern Illinois. Between 8,000-7,000 y B.P. there was an eastward increase in prairie-forb pollen in northcentral Minnesota and southern and western Wisconsin but a decrease in northern Illinois. By 6,000 y B.P. there was continued retreat of prairie in

Illinois and also in northern Minnesota, yet prairie remained at its eastern extreme in southeastern Minnesota and southwestern Wisconsin. From 6,000-3,000y B.P. prairie-forb pollen in northern and western Minnesota decreased as prairie retreated to the west. At this same time there was an eastward advance of prairie in central Illinois, indicated by an increase of prairie-forb pollen in Iowa, Illinois and northern Indiana. Jones and Beavers (1964a) estimate that a period of 5133 years of prairie vegetation was required to accumulate the quantity of opal phytolith material present in the soils of central Illinois. Prairie vegetation established early in this period would have the time necessary to produce this volume of opal.

This renewed expansion of prairie vegetation along the Prairie Peninsula may be an important event with regard to species migrations. Relatively early in this period (6,000-3,000 y B.P.) the levels of Lakes Huron and Michigan had crested at the high Nipissing stage and then gradually through time had dropped to their present positions. Any prairie species that were able to disperse along lakeshores and water courses would have found newly exposed and uncolonized substrate available to them. The distribution of many prairie species today along lakeshores and water courses is an indication of this dispersal pattern. It was also during this time period that the Maxton Plains began to emerge from Lake Huron.

After 3,000 y B.P. the prairie border moved westward in the south but was stable in the north (Webb *et al*. 1983).

This westward movement was the result of a slow but persistent invasion of the prairies by deciduous forest taxa (Geis and Boggess 1968). It is easier to understand the basis of the disagreements as to the details of the prairie-forest vegetation changes when it is clear that the events were asynchronous from region to region.

Climatic changes.

Climatic changes are often invoked to explain changes in vegetation. That this is not always so has been recognized by many authors and clearly demonstrated most recently by Davis (1983) in her illustration of differential rates and directions of migrations of boreal and deciduous forest taxa. The eastward expansion of the prairie is generally accepted to have been the result of climatic changes. The exact nature of these changes has not been agreed upon, with periods of warmer and/or drier conditions being proposed. The term "Hypsithermal" for this interval is now the most widely accepted in North American literature, with xerothermic, altithermal, megathermal and others rejected for various reasons (Deevey and Flint, 1957). Much of the confusion as to terminology and interpretation comes from the fact that: 1) it is difficult to separate the effects of temperature and precipitation 2) many of the early ideas of climatic changes in northeastern United States came from the European literature where a "climatic optimum" of warm and moist conditions during the

Atlantic was to have been followed by the Sub-Boreal with a thermal maximum of 2-3°C. above present (Deevey and Flint, 1957; Wright, 1968a). Since it was believed by Deevey and Flint and others that the effects of temperature were primary, the terms for this period of climate change reflect the supposed importance of this climatic parameter. Wright (1968a) notes that the interpretation of a "climatic optimum" preceding the Hypsithermal in North America cannot be justified.

That the Hypsithermal was not a uniform event either geographically or temporally is now becoming apparent. Wright (1976) notes that it is valid to identify a Hypsithermal interval of continental dimensions but with rather indefinite temporal boundaries. He suggests that it lasted over a longer interval farther to the south and west than it did in the northeast. Watts and Winter (1966) present evidence that, in Minnesota, the Hypsithermal consisted of at least four intervals of dry conditions, each lasting several hundred years. Bryson (1983) also noted that this was not a uniform climatic period; rather the Hypsithermal had a distinctly different midsection and was not constant throughout the range. Another interesting observation by Bryson is that the period from 7,000-3,000 y B.P. was a time of enhanced volcanic activity around the world and that this may have been an important influence on climate.

Recent work of Dean _et al_. (1984) in northwestern

Minnesota allows an independent (non-palynological) look at climatic changes over the past 10,400 years. They present a sedimentological analysis of varved lake deposits from Elk Lake, Minnesota. Their results show that the mid-Holocene dry interval between 8,500 and 4,000 y B.P. was actually asymmetrical and that it actually consisted of two distinct drier pulses, separated by a more moiste interval. They conclude that: 1) amplitudes of climatic oscillations were greatest during the prairie period; 2) cyclic fluctuations were abrupt and persisted throughout the Holocene, being most clearly recorded within the two drier periods; 3) there is evidence for both gradual and abrupt, short term climatic changes; and 4) climate stabilized in northwestern Minnesota around 3,500 y B.P. They suggest that the prairie period was drier than present, but evidence is somewhat equivocal as to whether it was colder or warmer.

The recent work of Bartlein _et al_. (1984) provides a less subjective approach to determining climatic changes as represented in palynological data. They use multiple regression models to establish relationships between modern vegetation, as represented by modern pollen spectra, and associated climatic parameters. They then apply these relationships to fossil pollen data. From this analysis they note several broad-scale vegetational changes that can be interpreted in climatic terms: 1) an early Holocene northward movement of spruce forest and later southward movement after 3,000 y B.P. 2) an eastward movement of the prairie-forest border into southwestern Wisconsin by 8,000y

B.P. and later westward retreat after 6,000 y B.P. Several climatic changes that were postulated include: by 6,000 y B.P. precipitation was less than 80% of present (in Wisconsin and Minnesota); after 6,000 y B.P. precipitation generally increased throughout the region while temperature decreased in the north and increased in the south; the time of maximum temperature varies within the midwest, being earlier in the north and later in the south.

Two major assumptions required for this approach should be mentioned since a violation of them could present significant difficulties. These are that: 1) vegetation represented by the modern pollen data must be in equilibrium with modern climate 2) variation in pollen data must be attributable to climate. Of significance to these assumptions is the recent the work of Davis (1983) in which she shows that some vegetation changes are not due to climate, but rather to differential migration rates. This means that not only will it not be possible to attribute all variation in pollen data to climate, but that some parts of the modern vegetation probably are not yet in equilibrium with climate. In spite of these limits, this study provides some indication of temperature and precipitation changes.

A final factor that should be considered here because of its affects on vegetation and because of its link, at least on a regional scale, to climate, is fire. Many palynological studies indicate that fire has been a factor in the history of the vegetation being examined. This is particularly true of the Prairie Peninsula region, though it has also been a significant factor throughout postglacial time in the region north of Lakes Superior and Huron (Terasmae, 1967). The importance of fire in the Prairie Peninsula has been mentioned by Transeau (1935), Borchert (1950), Cushing (1965) and Webb *et al*. (1983). Transeau felt that fire has favored persistence of prairie species but that it was not a factor in the origin of the Prairie Peninsula. In contrast, Cushing states that fire was important in pushing back the forest and maintaining the prairie-forest border. Webb *et al*. (1983) note that, in southcentral Minnesota, the dominating local controls of the prairie-forest boundaries were topography, soils and especially fire, which they assert was often set by Indians. They also note that, though these are the proximal factors in controlling the exact timing and local expression of vegetation changes, climate is the ultimate cause for vegetation changes on a regional scale. This conclusion is quite interesting, however it is not really new since it is essentially the same conclusion, albeit much more refined, as wes reached by Cowles (1928) and earlier scientists.

In a study of the vegetational history of the eastern Upper Peninsula of Michigan, Futyma (1982) notes several interesting events that pertain to the importance of fire. In this region the Hypsithermal is indicated by the peak abundance of *Pinus strobus* and the synchronous low levels of *Picea* and hardwoods from 7,000 to 5,000 y. B.P. By about 5,000 y. B.P. there was a regional increase in hardwood

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species. These deciduous taxa became the dominants in areas of loamy soil. Dominance of Pinus was maintained on drier, sandier soils. Futyma notes that the dominance of pines is not so much an adaptation to drought as it is to fire and that under the influence of the Hypsithermal climate, all sites experienced fires at a frequency sufficient to favor dominance of pines. Futyma (1982) suggests that temperature decreased between 6,000 y. B.P. and 2,500 y. B.P. in eastern Upper Michigan and that the resulting decreased moisture stress would have favored dominance by deciduous taxa on soils with good moisture holding capacity. He concludes that the vegetation on fine textured soils shows a greater response to climatic changes than does vegetation on sandy soils.

This discussion of the late-glacial and Holocene vegetation history and the climatic changes that are hypothesized to have been driving forces during this time in the Great Lakes region should provide the background necessary for evaluating the unusual aspects of the vegetation of the alvars of Drummond Island. It is particularly important to note the coincidence (during the 6,000-3,000 y B.P period) of the strong eastward migration of prairie elements, in the Illinois, northern Indiana and southern Michigan region, with the final lowering of water levels in Lakes Michigan and Huron after the Nipissing high.

ALVARS AND ALVAR VEGETATION.

Alvar as a geomorphological and ecological term.

Published use of the term "alvar" in describing a geomorphological setting, and sometimes the associated vegetation, can be traced back to the time of Linnaeus, from a report (1745) on a trip to the island of Öland, off the southeastern coast of Sweden in the Baltic sea (Konigsson, 1968). In the North American literature this term is poorly known but appears to have been used here by Beschel and Catling *et al.* (1975).

Alvar has its origin as a Swedish word, being variously defined in Swedish and Estonian dictionaries as a limestone region covered with thin soil and stunted vegetation (Saagpakk, 1982). The root of the word, "alv", refers to the subsoil or subsurface. Alvar is defined in a recent dictionary of ecological, evolutionary and systematics terms as a "plant community dominated by mosses and herbs occurring on shallow alkaline limestone soils" (Lincoln *et al.*, 1983).

Alvar is not used to describe any single plant community or association. Rather, it is used to describe a physical setting that is one of essentially flat limestone with thin soil, supporting only scant, open vegetation (Pettersson, 1965; Konigsson, 1968). Because of the unique physical setting, alvars usually have an unusual flora associated with them. Rosen (1982) and others frequently use "alvar" as an adjective in connection with the vegetation found on these limestone barrens. Alvar, then, refers to the physical setting as described above, and alvar vegetation refers to the unique plant assemblages that are characteristic of these areas. These plant assemblages will be addressed in detail following a discussion of the physical features of the North American and Swedish alvars.

Description of the physical features of the alvars of the Maxton Plains.

As mentioned earlier, the bedrock of the Maxton Plains of Drummond Island is composed of dolomitic limestone. The surface of this substrate is quite flat and slopes to the southeast with gradients of one percent or less. Deposits of glacial till on the Maxton Plains are generally quite thin to absent, though there are numerous glacial erratic boulders distributed throughout. Soils on the alvar sites are also minimal, ranging in depth from zero to 15 cm. The lack of till may be the result of wave action and flow patterns associated with the great fluctuations in lake levels that alternately inundated and exposed Drummond Island through much of the early Holocene.

There are several small, but topographically significant, ledges or scarps (1-2 meters in height) which face northward and which extend in an east-west orientation, roughly conforming to the north shore of the island. Since the bedrock surface slopes gently to the southeast, these ledges have a damming effect on water drainage.

Another feature of the bedrock that is important to the hydrology of the Maxton Plains is a prominent jointing pattern. These nearly vertical joints are filled with degraded dolomite and soil and can be several centimeters wide at the surface and likely extend to a considerable depth. The significance of the joints can be easily recognized since rows of trees, shrubs or grasses that are much more luxuriant than the surrounding vegetation are usually associated with them. These joints provide an important source of water that can be seen by observing the road surface in the early morning where it crosses a system of joints. Even through extended dry periods the soil and rock surface adjacent to a joint is usually quite damp, whereas surface areas between the joint sets are dry.

The elevation of the alvars of the Maxton Plains is only slightly higher than that of Lake Huron, which is 580 ft. The alvar sites range in elevation from approximatly 585 ft. to 625 ft. with the most extensive areas at 590 ft. to 615 ft.

Fire appears to be an occasional factor in the history of the Maxton Plains region. A Michigan Department of Natural Resources Information Circular (1947) reports that a large fire occurred on the Maxton Plains about 1925. In a compilation of the history of Drummond and the surrounding islands, Ashley (1978) noted a "...forest fire that swept the island..." on 25 June, 1820. The extent of this fire is not known. Present evidence of past fires include pieces of charcoal in the soils, especially near upland edges, and burn marks on dead stumps, both along the edges and in the open alvars. Frequency of fires, however, is not known. Also unknown is what influence Indian cultures have had on this area.

A physical factor that perhaps should have been considered is frost action but evidence to demonstrate the significance here was not pursued. Alternate freezing and thawing can have a major influence on the rock, soil and plants of a region.

Soils of the Maxton Plains alvars.

Methods.

Composite soil samples were collected on 19-21 July 1983 from all alvar sites where vegetation was sampled. In site #29-2 (see Figure 18, Appendix A.) soil samples were taken adjacent to each vegetation sampling plot so that the variability of soil parameters within a site could be assessed. Samples were stored in sealed plastic bags until returned from the field. Soil depth was measured by probing each 1/4 M^2 plot at the corners and center with a calibrated steel pin. The pin was driven into the soil until it reached bedrock. Soil moisture was measured as percent of fresh weight after drying 24 hours at 100° C. Organic content is measured as percent of soil dry weight after combustion at 550° C. for four hours. Organic content may be overestimated because of the high carbonate component of the soils. Soil pH was measured using an Orion 199 A pH meter after soaking equal weights of fresh soil and distilled water (20 g.) for one hour. Soil texture was determined by the Bouyoucos method of suspending a sample of soil (50 g.) in water and measuring the amount of soil remaining in suspension after 40 seconds (silt and clay) and two hours (clay) with a calibrated hydrometer.

Results.

The soils of the alvar sites are quite thin, with average depths ranging from 4.7 cm. to 12.9 cm. The soils are dark brown to black in color with high organic contents, ranging from 12.8% to 27% ash-free dry weight. The average soil texture is a silt loam. Soil samples have high sand and silt fractions and a very minor clay fraction. Soil pH is circum-neutral with values ranging from 6.5 to 7.1. Table 1 presents measured soil parameters for all sites. Table 2 presents the range of variation for moisture, organics and pH measured in site #29-2.

Summary of the climatic data for Drummond Island.

The climate of the Maxton Plains region was characterized from weather records (Michigan Dept. of Agriculture Weather Service, East Lansing, Michigan) from De Tour Village, at the eastern tip of the Upper Peninsula. It

Table 1. Summary of soil data for the eleven sites where vegetation has been sampled.

Summary of Soil Data for the Maxton Plains Alvars

Site	Percent Moisture	Percent Organics	pH	Mean Depth	Soil Texture		
					Sand	Silt	Clay
28/29-1	13.67	27.04	7.0	8.77	38	58	4
28/33-1	8.38	23.74	7.0	9.25	44	51	5
29-2	8.23	18.11	7.0	9.73	54	41	5
33-2	11.49	23.75	7.1	7.55	34	60	6
33-4	9.54	32.75	6.8	7.57	32	63	5
34-1	7.07	17.95	6.8	4.67	24	72	4
34-2	10.29	18.75	7.0	12.90	44	49	7
34-3	7.59	17.96	6.5	10.35	36	56	8
34-5	6.26	16.35	6.9	6.75	20	77	3
36-6	8.94	12.76	7.0	9.24	40	48	12
36/31-1	7.69	15.96	6.9	9.99	36	61	3

collection date:	sites:
18 July 1983	29-2, 28/28-1
19 July 1983	33-2, 33-4, 28/33-1
20 July 1983	34-2, 34-3, 36/31-1
21 July 1983	34-1, 34-5

Table2. Soil data from site #29-2 showing variability of measured soil parameters.

Variability of Soil Parameters Within a Site.

Sample Number	Percent Moisture	Percent Organics	pH
T1-#1	5.90	13.98	7.1
T1-#2	6.94	14.53	7.0
T1-#3	7.22	18.07	7.1
T1-#4	8.53	19.37	6.9
T1-#5	8.49	19.69	7.1
T2-#1	7.79	19.79	7.0
T2-#2	7.37	18.52	7.1
T2-#3	9.46	20.62	7.2
T2-#4	12.04	21.08	7.0
T2-#5	5.29	12.48	7.1
T3-#1	5.40	14.11	7.1
T3-#2	6.45	18.26	7.1
T3-#3	10.26	21.56	7.1
T3-#4	9.69	17.21	7.1
T3-#5	10.94	24.02	7.1
T4-#1	9.02	18.68	7.0
T4-#2	7.57	14.48	7.1
T4-#3	10.94	19.32	6.6
T4-#4	6.65	14.00	7.1
T4-#5	8.30	15.01	7.1
T5-#1	8.09	16.69	7.0
T5-#2	7.89	15.52	7.1
T5-#3	7.50	16.50	7.2
T5-#4	5.11	13.35	7.1
T5-#5	11.40	27.53	7.0
T6-#1	6.88	16.75	7.1
T6-#2	10.16	23.71	7.1
T6-#3	9.93	22.74	6.0
T6-#4	8.08	17.99	6.3
T6-#5	7.63	17.92	7.1
Mean	8.23	18.11	7.0

Soil samples were collected on 18 July 1983.

should be noted that the De Tour weather station is located immediately adjacent to the water. Therefore temperatures recorded may be more moderated than those on the Maxton Plains. Precipitation should not be so affected. Table 3 presents mean annual temperatures (min., max. and mean) and precipitation for 1964 through 1983, as well as a 20 year average for these values. The coldest month is February with a mean temperature of -9.24°C. The warmest month is July with a mean temperature of 19.09°C. The value T.max./Ppt. is a relative measure of moisture availability. A larger value indicates higher than average temperatures and/or lower than normal precipitation. This value, however, utilizes annual precipitation which will obscure summer drought conditions if winter precipitation is high. Further, heavy winter snows are of little importance in recharging the soils, considering their shallow depth and the bedrock substrate.

Table 4 summarizes climatic data for the critical period, June through September. In this table, Tmax./Ppt. is calculated using temperature and precipitation values for the critical period. Using these values the dry summers of 1966, 1976 and 1983 are obvious.

The summer of 1983 was very warm, the warmest on record for the 21 year period, with an annual mean maximum temperature of 11.6°C., 1.1°C. above the average. The mean temperature for July 1983 was 22.6°C., 3.5°C. above the average of 19.09°C. Precipitation in 1983 was below normal with 731.3 mm. recorded at De Tour. Precipitation during

Table 3. Summary of the climatic data for De Tour village from 1964 to 1983.

SUMMARY OF CLIMATIC DATA FOR DE TOUR VILLAGE
1964-1983

	MEAN ANNUAL TEMPERATURE			MEAN ANNUAL PRECIPITATION	
YEARS	Tmax.C.	Tmin.C.	TmeanC.	Ppt.mm.	Tmax./Ppt.
1964	11.4	-.27	5.565	786.9	.0145
1965	10.2	-.47	4.865	831.3	.0123
1966	10.6	.42	5.510	630.4	.0168
1967	10.0	-.77	4.615	757.9	.0132
1968	10.0	-.03	4.985	865.1	.0116
1969	10.7	.35	5.525	731.0	.0146
1970	10.6	-.13	5.235	909.8	.0116
1971	10.7	.20	5.450	831.8	.0129
1972	9.4	-.86	4.270	762.0	.0123
1973	11.2	1.95	6.575	750.1	.0149
1974	10.0	.26	5.130	745.5	.0134
1975	11.4	1.20	6.300	691.1	.0165
1976	10.5	-.23	5.135	590.3	.0178
1977	10.5	.83	5.665	851.9	.0123
1978	10.0	.26	5.130	725.2	.0138
1979	9.4	.23	4.815	935.5	.0100
1980	10.1	.22	5.160	564.4	.0179
1981	11.1	.94	6.020	581.2	.0191
1982	10.3	-.10	5.100	797.8	.0129
1983	11.6	1.70	6.650	731.3	.0159
20 YR. AVE.	10.485	.285	5.385	753.53	.0142

MEAN MONTHLY TEMPERATURE (C.) FOR:

FEBRUARY (coldest month)	-9.24
JULY (warmest month)	19.09

Table 4. Summary of the climatic data for the critical period of June through September.

SUMMARY OF CLIMATIC DATA FOR THE CRITICAL PERIOD
JUNE-SEPTEMBER

YEAR	MEAN MAX. TEMPERATURE (C.)	MEAN PRECIPITATION (mm.)	Tmax./Ppt.
1964	22.15	292.8	.0756
1965	21.00	402.2	.0522
1966	23.22	157.0	.1479
1967	22.22	267.2	.0832
1968	22.32	385.5	.0579
1969	22.50	320.0	.0703
1970	23.28	493.2	.0472
1971	22.35	277.6	.0805
1972	21.35	344.9	.0619
1973	22.48	325.9	.0690
1974	21.65	308.5	.0702
1975	22.68	286.9	.0790
1976	23.35	225.3	.1036
1977	21.00	383.1	.0548
1978	21.15	389.9	.0542
1979	21.30	350.2	.0608
1980	22.05	232.0	.0950
1981	22.82	234.6	.0973
1982	21.10	307.2	.0687
1983	25.40	220.6	.1151
20 YR. AVE.	22.26	310.2	.0718

the critical growing period was the second lowest on record for the 20 year period with 220.6 mm. measured, 89.6 mm. below normal. Signs of drought conditions were well developed in August, with dead *Picea glauca* trees and severely damaged *Populus tremuloides* and *Juniperus communis* individuals. The only grasses and other herbaceous plants that werenot severely damaged by the dry conditions were associated with joints in the bedrock. With weather conditions as such, the 1983 season was not an ideal one for characterization of the vegetation. The late season species were the most severely affected by the drought and thus, the least accurately represented in the analysis.

Comparison of the Maxton Plains alvar setting with alvars of other regions.

The physical features described above for the alvar sites of the Maxton Plains are very similar to features of the alvars of Ontario, Canada, as well as to those of Öland and Gotland, Sweden. Catling *et al*.(1975) described the vegetation associated with several alvar sites in southern Ontario. These sites include Manitoulin Island and the Bruce Peninsula which, togeather with Drummond Island, are located along the Niagara escarpment. Other sites in Victoria, Peterborough, Hastings, Lennox and Addington Counties (Ontario) are situated on limestone, along the contact lines between Ordovician and Precambrian strata. It is not surprising that the sites Catling *et al*. (1975)

described from Manitoulin Island and the Bruce Peninsula are very similar to those on the Maxton Plains since they all have a similar dolomitic limestone substrate and are located in relative close proximity, thus likely sharing a similar postglacial history. The sites along the contact lines are similar to those on the Maxton Plains in that they are also situated on limestone plains and have been greatly influenced by deglaciation events and lake level fluctuations (Harrison, 1971; Chapman and Putnam, 1966).

The Great Alvar of Öland, Sweden is quite similar to the alvars of Drummond Island in several respects. Pettersson (1965) notes that the islands of Öland and Gotland are composed of calcareous Cambro-Silurian strata. The limestone bedrock outcrops in many places on Öland, with the most extensive areas being on the southern part of the island where the Great Alvar (or Stora Alvaret) is located. The bedrock dips to the east-southeast with a shallow gradient. A scarp system runs roughly north-south and faces westward. The scarps serve to dam surface drainage and form shallow lakes and fens.

Glacial till deposits are very thin and soils are poorly developed over much of the Great Alvar. Areas of exposed bedrock are not frequent on the Great Alvar but there are local exposures. It is assumed that till cover on southern Öland was originally very thin and that it was later worked by wave action, which removed all but the coarse material which was deposited in beach ridges (Rosen, 1982). These beach ridges demonstrate the influence of the Baltic Sea on landscape development.

There is also a prominent joint system developed in the bedrock of Öland. The bedrock is limestone and therefore much more soluable than dolomite. The joint system is much more developed on Öland than it is on the Maxton Plains and, in fact, displays characteristics of karst topography. The joints on Oland are important in the hydrology of the region in that water drainage follows these systems underground (Konigsson, 1968). When filled with soil, these joints can also provide an important source of water during dry periods (Rosen, 1982). In a pattern similar to that on the Maxton Plains, narrow strips of trees, shrubs and harbaceous plants can be seen growing along these structures (Pettersson, 1965; Konigsson, 1968).

The climate of Öland can be compared to that of the De Tour Village area. From Table 5 it can be seen that the mean annual temperature at De Tour is only 1 - 1.5°C. lower than that measured at Ekerum, near the Great Alvar. The moderating effect of the Baltic Sea can be clearly seen by comparing the mean temperatures for the coldest month (February) and the warmest month (July) for the two localities. Pettersson (1965) notes that Öland lies in the rain shadow of the southern Swedish uplands and thus is sheltered from the moisture-bearing Atlantic fronts. Most of the moisture that is received by Öland and the east coast of Sweden comes from the south and the east. Because of the low elevation of Öland (57 m.a.s.l. maximum) much of the

Table 5. Comparison of climatic data for De Tour Village and Öland, Sweden.

COMPARISON OF CLIMATIC DATA FOR
DE TOUR VILLAGE AND OLAND, SWEDEN

	MEAN TEMPERATURE (C.)			MEAN PRECIPITATION (mm.)	
	ANNUAL	FEB.	JULY	ANNUAL	APR.-SEPT
De Tour (1964-1983)	5.4	-9.2	19.1	753.5	441.27
Öland-Ekerum (1921-1950)	7.0	-1.8	17.1	463 *	249 **
(1969-1971)	6.5	-2.8	17.0		

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* precipitation measured at Skogsby (1965-1979)
** precipitation measured at Skogsby (1968-1980)

Climatic data for Öland from Rosen (1982).

moisture-bearing air passes over. This can be seen by noting that the annual precipitation value reported from Öland's Skogsby Ecological Station is only 61% (463 mm.) of that reported from De Tour (753.5 mm.). Another significant difference between the two localities is that Öland, being at approximatly 57° N. latitude will receive longer daylight hours during the summer months than will the Maxton Plains at 46° 05' N.

These climatic variables show that, though mean annual temperatures are comparable, there are major differences in temperature extremes and precipitation. Pettersson (1965) notes that the precipitation and temperature conditions on Öland are irregular and that they can cause great annual differences in the occurrence of many species. Similarly, the weather conditions on the Maxton Plains are also variable and a comparable affect on the vegetation can be expected.

Maxton Plains alvar vegetation.

Introduction.

The vegetation of the Maxton Plains is primarily dominated by coniferous forest. On well drained sites *Picea glauca*, *Populus tremuloides*, *Abies balsamea* and *Thuja occidentalis* dominate, while on poorly drained sites *T. occidentalis*, *Populus balsamifera*, *Fraxinus nigra* and *Larix laricina* dominate. The vegetation of the remainder ofthe island is a mixture of northern hardwoods and boreal forest (Stephenson, 1983). The grass and sedge dominated alvar sites occur both as distinct openings in the forest and as a more or less continuous band of varying width, extending eastward for several kilometers from the southwest end of the Maxton Plains on Potagannising Bay, (see Appendix A for a map of the alvar sites of the Maxton Plains).

The vegetation of the alvar sites is interesting in several respects. The distribution pattern of the vegetation in a site is usually predictable because of the nature of the rock substrate. Since the bedrock surface slopes gradually to the southeast and since the lowland boundary is usually sharply defined by a scarp or ledge oriented roughly perpendicular to the slope, the southern edges of the alvar sites are usually poorly-drained wetlands dominated by Carex ssp. or lowland forest. The upland edges are not as sharply defined. They are gradual, usually with a transition zone dominated by Populus tremuloides and sometimes Picea glauca. Juniperus communis is an important understory dominant. This transition zone is quite variable in width, ranging from approximately 20 m to 100 m or more. Sometimes these upland transition zones are dominated by a zone of young Populus tremuloides. These broad zones of young aspen have the appearance of having encroached relatively rapidly. The zones of encroachment are of particular interest in the investigation of vegetation changes on the Maxton Plains. Features of the bedrock are also likely important in defining the position of these upland boundaries.

The dolomite exhibits a network pattern of vertical joints which range in width from less than 1 cm to 3 cm across at the surface. Individuals of *Picea glauca*, *Juniperus communis*, *Shepherdia canadensis* and other woody members of the upland transition that become established and persist in the open alvar are usually associated with a joint.

Another feature of the bedrock that is also probably important in determining vegetation patterns is the tendency of the dolomite to fracture along horizontal planes, more of less parallel with the bedding, forming slabs of rock that are variable in thickness and size. There may be several layers of these slabs, each separated by a thin band of degraded dolomite, above the unweathered bedrock. It seems likely that this exfoliation is a result of frost action, as moisture gradually penetrates zones of weakness in the rock. The degree of development of this horizontal fracturing and slab formation may be related to position on the slope. It appears that this feature is most strongly developed in low, poorly-drained areas. In better-drained areas, such as the upland transition zone, frost action seems to result in smaller and thinner, irregularly shaped dolomite fragments. This variation, however, may not be entirely due to drainage, as there are lithologic features of the rock that may also be important. Spaces between these rock slabs are filled with degraded dolomite and thus are important as potential zones for rooting. The nature and position of the upland transition zone may also be related to these structures.

Between the more or less abrupt lowland wet edges and the broader upland transition zone is an open, treeless area usually dominated by *Sporobolus heterolepis* and *Schizachyrium scoparium*, both C_4 grasses, and *Eleocharis compressa*. The vegetation and history of these grasslands are the primary foci of this study. The same physical features that appear to be important in determining the nature of the upland transition flora are also likely important in the open alvars. For example, the importance of the joints in providing a source of moisture can be easily observed since the tallest and most luxuriant growth is associated with a joint.

There are frequent, small, shallow, rectangular depressions (as much as 10 cm deep and several dm across) distributed throughout the alvars. These depressions tend to retain moisture longer and thus impart a small scale mosaic pattern to the vegetation. There are occasional larger depressions, not associated with the scarps and lowland edges, that retain water for longer periods of time. These areas may be as much as a meter in depth and several tens of meters across. The species assemblages in these larger depressions may be very similar to those near the lowland edge of the alvars. Since the larger depressions support different species assemblages than the remainder of the alvar areas, the vegetation in these depressions is excluded from all analyses and surveys of alvar vegetation.

There are several areas with no soil. These "pavement" or outcrop areas are well developed in the large sites (site numbers 34-1 and 34-5) in section 34 (T43N, R6E) and in section 20 in the sites along the northwest shoreline. In such pavement areas vascular plants can grow only in association with joints. The areas between joints are usually bare rock. Wind-blown soil can accumulate along these lines of vegetation, allowing gradual colonization of the open areas. Various species of mosses will sometimes colonize the shallowest soil deposits.

Many of the alvar sites contain inclusions or islands of trees, usually consisting of *Picea glauca* and *Populus tremuloides* but sometimes also including *Thuja occidentalis* or *Abies balsamea*. These tree islands are usuallyassociated with some kind of topographic or substrate irregularity. Typically there is a band of aspen encircling the margins of such tree islands.

Floristic composition of the alvars.

The floristic composition of the alvars of Drummond Island is of interest primarily because of the unusual assemblage of plant species found there. Appendix A is a map of the Maxton Plains with all alvar sites numbered. Appendix B presents a checklist of the taxa found on the alvars. This listing also includes synonymies and notes on significant distribution patterns. Appendix C is an alphabetical listing of species by genus. Stephenson (1983) noted that two major floristic elements contribute most of the vegetation cover in these areas. These are: 1) an arctic and/or boreal-cordilleran group and 2) a midcontinental group. A third element, though of lesser importance with regard to cover, consists of a southern and eastern group of species.

In an attempt to look further at the biogeographic affinities of the alvar flora, the following references were consulted for information regarding distribution patterns: Gleason and Cronquist (1963), Fernald (1950), Hulten (1968). In this study the biogeographic affinity of a species is taken to be represented by the center of its present distribution. It should be noted that there are several species with a significantly disjunct occurrence on the Maxton Plains. Disjunct northern species include: *Carex scirpoidea* and *Trisetum spicatum*. Disjunct midcontinental species include: *Geum triflorum* and *Sporobolus heterolepis*. Following is a listing of species according to biogeographic affinity. For a discussion of the importance and relationships of species and floristic elements in the vegetation see the discussion in "Vegetation Analysis".

Species of midcontinental affinity.

Anemone canadensis
Apocynum sibiricum var. *cordigerum*
Aquilegia canadensis var. *hybrida*
Aster ptarmicoides
Bromus kalmii
Carex crawei
Carex merritt-fernaldii
Carex richardsonii
Carex umbellata

Castilleja coccinea
Cirsium hillii
Comandra umbellata
Erucastrum gallicum
Geranium bicknellii
Geum triflorum
Polygala senega
Ranunculus fascicularis
Rhus aromatica
Rhus glabra
Rosa blanda
Schizachyrium scoparium
Scutellaria parvula
Smilacina stellata
Sporobolus heterolepis
Sporobolus vaginiflorus
Trichostema brachiatum
Verbena simplex

Species primarily of northern and cordilleran regions of North America.

Aster ciliolatus
Carex viridula
Epilobium ciliatum
Juncus dudleyi
Juniperus horizontalis
Ribes oxyacanthoides
Rosa acicularis
Senecio pauperculus
Shepherdia canadensis
Sisyrinchium montanum
Symphoricarpos albus
Viola nephrophylla

Circumboreal species (some with interrupted distributions).

Achillea millefolium ssp. *lanulosa*
Agropyron trachycaulum
Arabis hirsuta var. *pycnocarpa*
Arctostaphylos uva-ursi
Artemisia campestris ssp. *caudata*
Botrychium simplex
Campanula rotundifolia
Carex scirpoidea
Cerastium arvense
Deschampsia cespitosa
Juniperus communis
Lathyrus palustris
Poa pratensis
Potentilla anserina
Potentilla fruticosa
Potentilla norvegica

Triglochin maritima
Trisetum spicatum var. molle

Eastern and Great Lakes region.

Amelanchier sanguinea
Aster pilosus var. pringlei
Carex castanea
Carex garberi (primarily Great Lakes region)
Carex laxiflora
Dichanthelium accuminatum
Eleocharis compressa
Hypericum kalmianum (primarily Great Lakes region)
Prunus pumila var. depressa
Prunus virginiana
Satureja glabella var. angustifolia
Saxifraga virginiensis (northern if synonym with S. nivalis)
Solidago nemoralis
Solidago ohioensis (primarily Great Lakes region)
Vitis riparia
Zigadenus glaucus

Species widespread within North America.

Agrostis hyemalis
Ambrosia artemisiifolia
Antennaria neglecta
Apocynum androsaemifolium
Arenaria stricta
Carex interior
Danthonia spicata
Fragaria virginiana
Geranium carolinianum
Glyceria striata
Lilium philadelphicum
Silene antirrhina
Solidago canadensis
Veronica peregrina
Vicia americana

Species with a cosmopolitan distribution (or nearly so).

Cardamine parviflora var. arenicola
Equisetum arvense
Festuca ovina var. saximontana
Prunella vulgaris var. lanceolata
Pteridium aquilinum var. latiusculum
Satureja vulgaris

Introduced species.

Agrostis gigantea
Arenaria serpyllifolia
Barbarea vulgaris
Centaurea maculosa
Chrysanthemum leucanthemum
Cirsium arvense
Daucus carota
Hieracium aurantiacum
Hieracium piloselloides
Hypericum perforatum
Medicago lupulina
Phleum pratense
Plantago lanceolata
Poa compressa
Potentilla recta
Ranunculus acris
Rumex crispus
Taraxacum officinale
Tragopogon pratensis
Trifolium hybridum
Trifolium pratense
Trifolium repens
Verbascum thapsus
Veronica arvensis

Summary

Total number of species: 118

	Number of Species		Percent of Total	
Midcontinental		26		22.0
Northern		30		25.4
(Northern/Cord.	12		10.2)	
(Circumboreal	18		15.2)	
Eastern/Great Lakes		17		14.4
Widespread		21		17.8
(In North America	15		12.7)	
(Cosmopolitan	6		5.1)	
Introduced		24		20.3

From the summary of this listing it can be seen that the northern element is the largest with 30 species, followed by the midcontinental group with 26 species. Though the group of introduced taxa includes 24 species, it will be seen in the discussion of the vegetation analysis that many of these taxa are found only in disturbed sites and are represented there with low coverage values.

In an unpublished report to the Michigan Natural Features Inventory, Gereau (1980) provided a list of the mosses encountered on the alvars of the Maxton Plains. Included in this list are several circumboreal species including: *Grimmia alpicola* Hedw., *Tortella tortuosa* (Hedw.) Linpr., *Myurella julacea* Schwaegr. and *Scorpidium turgescens* (T.Jens) Loeske.

The alvars are able to support this hybrid type of plant assemblage, with both western and northern species assemblages as major elements, because of their unusual physical features. Since spring is usually cool and moist, growing conditions in the open alvar areas are adequate to support the growth of early season northern species. During the summer, conditions are much warmer and drier, supporting the western assemblage of species. The temporal separation of these assemblages is pronounced. With few exceptions there is no overlap in the time of maximum development between these two species assemblages.

The unique nature of the vegetation of the Maxton Plains alvars.

As noted above, the vegetation of alvar areas is unusual in several respects. The unique nature of the flora of the Maxton Plains has been recognized for some time. Winchell, in 1861 is reported to be the first to comment on the nature of the vegetation of Drummond Island (Hiltunen, 1962). More recently, Hiltunen (1962) provided a list of the more conspicuous species found on the pavement sites of the Maxton Plains and he noted that many of these species are infrequent or rare in the state. He also noted that the limestone pavement community is one of the most unique of all of the plant communities on Drummond Island. According to records of the Michigan Natural Features Inventory (Mason Bldg. Lansing) the flora contains a large number of unusual species. Following is a listing of species recognized by the MNFI as "threatened in Michigan" and "special concern in Michigan" In each of these categories the species are listed in approximate order of decreasing abundance.

Threatened

Sporobolus heterolepis
Eleocharis compressa
Carex scirpoidea
Geum triflorum
Trichostema brachiatum

Special Concern

Carex richardsonii
Verbena simplex
Cirsium hillii
Trisetum spicatum

Many of these species are rare in Michigan because they are disjunct populations and not because of any inherent ecological characteristics of the species. It is interesting to note that nowhere else in Michigan is there a plant assemblage known that is so strongly dominated (percent cover) by state threatened species.

Stephenson (1983) notes another unusual aspect of the alvar vegetation. Although northern Michigan lies well within the forested region of North America, along the southern edge of the northern conifer floristic province of Gleason and Cronquist (1964), the alvars are unique in that they support natural grassland communities, the only reported naturally occurring grasslands in northern Michigan. That these are natural assemblages will be taken up in a later section of this discussion. In Michigan, natural grassland communities are usually found in the central and southern portions of the Lower Peninsula and are considered to be outliers, associated with the Prairie Peninsula of Illinois and Indiana (Transeau, 1935; Geis and Boggess, 1968; Stephenson, 1983).

Curtis (1959) recognizes several grassland communities in Wisconsin. In his key to Wisconsin plant communities, Curtis recognized "bracken-grassland" as the only grassland community north of the tension zone. South of the tension zone, however, he recognizes three grassland communities on upland sites. Of these, his description of "dry prairie" as thin soils over bedrock or gravels: *Bouteloua* and *Schizachyrium scoparium* (and *Sporobolus heterolepis*) dominating, is the closest approximation to the conditions and vegetation on the Maxton Plains. The most significant difference is the lack of *Bouteloua curtipendula* as a codominant on the Maxton Plains and its replacement there with a strong dominance by *Sporobolus heterolepis* (see vegetation analysis in the following section).

This is not to suggest that the grasslands of the Maxton Plains represent the remnants of a formerly contiguous grassland community, connecting the Maxton Plains with the prairie communities of Wisconsin, Illinois or southern Michigan. Rather, these sites represent habitats with a physical setting very similar to that of the dry prairies considered by Curtis (1959). They likely owe the presence of these midcontinental dominants (*Sporobolus heterolepis*, *Schizachyrium scoparium*), as well as the many other lesser (in dominance) species of the same geographic affinity, to their dispersal characteristics and migration patterns (Curtis, 1959; Geis and Boggess, 1968) and to the changes in climate (Dean *et al*., 1984) and Great Lakes elevations and drainage patterns (Wayne and Zumberge, 1965; Lewis, 1968; Cowan, 1978 and others) that are known to have occurred in the early Holocene.

Comparison of the alvar vegetation of the Maxton Plains with the alvars of other regions.

Though the vegetation of the Maxton Plains alvars is unusual in terms of the mix of species belonging to widely differing biogeographic affinities and with regard to the occurrence of a natural grassland north of the tension zone where the zonal vegetation is forest, the alvar vegetation is not unusual when compared to the vegetation of other alvar regions. Catling *et al*. (1975) described a very similar type of vegetation from Ontario which includes species of both northern and midcontinental affinities. Most of the species of the two major biogeographic assemblages are found on both the Maxton Plains and the alvar sites of southern Ontario. There are several midcontinental species reported from the Canadian alvars that have not been found on the Maxton Plains. Prominent among them is Bouteloua curtipendula, a codominant of the dry prairies. This species was recorded, along with numerous other midcontinental species, at the Salmon River site, just north of Lake Ontario. One possible explanation of the high number of midcontinental prairie species at this site is that the shores of Lakes Erie and Ontario and the surrounding land may have been a major corridor for the eastward migration of prairie species during the expansion of the Prairie Peninsula. This corridor would have extended through southern Michigan and is likely roughly delimited by the isolated prairie localities in southern Michigan, northern Indiana and Ohio, i.e., the Prairie Peninsula outliers of Transeau (1935).

Catling et al. (1975) also discuss the possible role of fire in the alvar vegetation. They suggest that fire may play a key role in maintenence of the alvar vegetation since shallow and droughty soils and the surrounding coniferous forests are highly susceptible to burning. They suggest that fire, climatic extremes and soil ion concentrations may be key factors in preventing forest from replacing the open alvar vegetation. As was mentioned earlier, there have been several fires reported from the Maxton Plains and evidence of fire includes charcoal in soils and scars on the bases of some stumps. Though fire has been reported from these areas, its importance with regard to vegetation dynamics is not known.

Catling (1977) reports the discovery of a disjunct Skipper butterfly in the alvars of Great La Cloche Island, Manitoulin District, Ontario. He notes that Oarisma garita Reakirt. is an insect of an apparently cooler, more western and cordilleran environment and that its occurrence on Great La Cloche Island is 650 miles east of any previous record.

A more surprising similarity comes from a comparison of the alvar vegetation of the Maxton Plains with that of Oland, Sweden. The Great Alvar of Öland supports an open, primarily herbaceous vegetation with trees restricted to joints and areas of deeper soil. The Great Alvar is surrounded by a primarily deciduous forest, as opposed to the surrounding coniferous forest on the Maxton Plains (Pettersson 1965, Rosen 1982). Pettersson (1965) notes that it is not unusual to find species growing together that are of quite different biogeographic affinities. Konigsson (1968) recognized the following groups of exotic elements:

1) Siberian group
2) Southeastern European group
3) Southern European group
4) Southwestern European group
5) Northern European group
6) Endemic group

Species of the southern and eastern European regions are representatives of steppe vegetation and are the functional equivalents of the midcontinental species on the Maxton Plains. The other major element is the arctic and alpine assemblage, consisting of the Siberian and northern European groups. Pettersson (1965) notes that the arctic and alpine group is especially strong in the bryophytes and lichens.

Rosen (1982) notes that the alvar vegetation of Öland is a hybrid type of situation in that there are characteristics of both steppe and heathlands vegetation. He reasons that it cannot be considered steppe because there are major soil and climatic differences: 1) steppe has much thicker soil 2) there is no frost action in soils of the steppe 3) steppe vegetation is not as complex with heath-like parts dominated by dwarf shrubs, mosses and lichens. Similarly, the vegetation cannot be considered heathlands because the widespread annuals that are present on the Great Alvar are almost absent in heathlands.

Finally, Konigsson (1968) notes that fire has been a factor in the history of the Great Alvar. Evidence of this comes from the sediments that he examined in his palynological study. It should be noted, however, that the Great Alvar has been subjected to human impact for a long time (at least since the Early Neolithic ca. 2800 B.C.) and that much of the fire history could be of human origin.

This comparison shows that, though compared to the vegetation of surrounding regions, alvars have an unusual assemblage of species, but when compared among themselves, alvars show many consistent patterns in floral composition, functional biogeographic affinities and vegetation structure.

Naturalness of alvar vegetation.

Evidence to support the assertion that the alvar vegetation of the Maxton Plains, as well as that of other regions, is natural comes from a variety of sources. Stephenson (1983) noted that the original land survey records of John Mullet in 1845 suggest that little has changed in the Maxton Plains area since that time. In addition, results of the vegetation analysis (see following section) suggest that the introduced weedy species have a negative affect on the native species of the alvars. Restriction of the sites so affected to areas of the Maxton Plains that are known to have been impacted is strong evidence for the assertions that the alvar areas are natural and that a majority have been minimally disturbed.

Similarly, Catling *et al*. (1975) suggested that the rich flora and the presence of many locally rare prairie species is evidence to support the postulated that the alvars are of natural occurrence and relict. They also note that the importance of Indian activity, primarily burning, in maintaining the "prairie vegetation" should not be overlooked.

The work of Warner (1980) on Manitoulin Island also suggests a natural origin for the limestone pavements and prairie-type communities of that region. He believes that the insular character, poor soils, local climate and periodic fires have retarded the rate of forest succession on Manitoulin Island and have perpetuated the existence of the unusual vegetation.

The degree of naturalness of the alvars of Öland has been in question for some time. Konigsson (1968) noted that since the time of Linnaeus (1751) naturalists and palynologists have been interested in the history of the alvar. In his summary of previous paleoecological studies, Konigsson noted that Erdtman saw a strong similarity between the modern alvar flora and the "pioneer phase" of the revegetation of the Swedish mainland after retreat of the glacial ice. He also noted that Iverson believed that the alvar was covered by a rather open forest during Boreal and Atlantic times, with elements of the present vegetation present in low numbers. It is the opinion of Konigsson that this open forest was primarily restricted to joint systems, thus dividing the large open areas of the alvar, which characterize the present condition, into many smaller units. The forest cover could not have been extensive because, as Pettersson (19650) suggested, a closed canopy may exterminate the heliophilous alvar vegetation much more effectively than would grazing.

As mentioned earlier, the Great Alvar has had a history of human presence for at least the past 5,000 years. Grazing of domestic animals and cultivation are suggested by Pettersson (1965) to be the primary sources of disturbance.

He notes that several members of the alvar flora had greatly increased in frequency and abundance in the areas where grazing pressure had ceased or diminished during the last century.

From this discussion it is clear that the flora of alvar regions is a natural assemblage of plant species. The degree of human impact on these communities is variable. In some areas, such as over a major part of the Maxton Plains there has been minimal disturbance. In other areas, such as the Great Alvar of Öland, human activities have had significant impact on native vegetation.

VEGETATION ANALYSIS.

Introduction.

There are many aspects to the vegetation of a region and the form of an analysis of that vegetation is dependent upon the goals of the study. There were four primary goals that were kept in mind during the course of the analysis of the alvar vegetation. These goals were: 1) provide an inventory of the alvars of the Maxton Plains in the form of species lists; 2) assess the degree of human disturbance for the sites examined; 3) develop an understanding of the composition and structure of the alvar vegetation; and 4) demonstrate the patterns of variation between sites.

There are four main aspects of the alvar vegetation that will be treated here. The methods involved in the investigation of each of these aspects will be outlined in the following section. These aspects are:

1) vegetation composition and variability between sites
2) similarity of the sites studied
3) relationships between biogeographic groups
4) relationship of species composition to size of site.

It was noted earlier, and should be restated here, that the growing season of 1983 was unusual in that it was drier and much warmer that usual. Drought damage was quite evident in August and some of the mid to late summer species may not be accurately represented (with regard to their "normal" importance in the community) in the vegetation sampling. The effects of the drought on the populations of three species, Sporobolus heterolepis, Carex scirpoidea and Geum triflorum, are discussed in detail elsewhere (Stephenson and Herendeen, submitted).

Methods.

1. Vegetation composition and variability between sites.

During the growing season of 1983 eleven alvar sites were selected for vegetation analysis. These sites were selected to include a wide range of sizes; those that were obviously much disturbed were excluded from this investigation. Figure 18, Appendix A, shows the locations and numbers of these alvar sites.

The vegetation was studied by means of quadrat sampling. The sample plots were 1/2 m x 1/2 m (1/4 m^2) and were located through stratified random sampling procedures. The longest dimension of each alvar site was measured. Six transects were then established roughly equidistant along and perpendicular to this line. The transects were divided into five 10 meter or 20 meter units such that the transects traversed most of the width of the site while avoiding, as much as possible, the transition areas. A sample was located in each segment of the transect by means of a randomly generated number between zero and nine (two random numbers added together for the 20 meter units). A total of

30 sample plots (6 transects with 5 samples in each) were thus established to evaluate the vegetation. In the smaller sites (34-2, 34-3 and 36-6) 10, 15 and 10 sample plots were used, respectively. The same sample locations were used throughout the growing season and exact locations of plots were marked by means of wood markers and colored toothpicks for the corners.

Dates for the various vegetation analysis activities in 1983 were as follows:

14-23 June- establish sample plots and measure coverage of flowering species

16-20 July- relocate sample localities and measure cover of flowering species; measure soil depths; collect soils for pH, organics and moisture

22-25 August- measure coverage of remaining species

11-12 September- check sample plots for late season species.

The sample quadrat used in June 1983 was a wood frame with internal dimensions of 1/2 m x 1/2 m. The quadrat was divided into 100 equal square units by a system of intersecting wires. This design allowed more accurate measurements of coverage of the small early season species. The sample quadrat used in July, August and September was also 1/2 m x 1/2 m but it was divided into quarters by two perpendicular wires. The taller vegetation of the latter part of the summer made the use of the initial sample quadrat impossible.

In sampling the vegetation, coverage was recorded for each species as close to its flowering time as possible. In this way the reported value is a measure of the maximum development of the species. Since many of the species are clonal grasses and sedges, measures of population densities, which require the identification of individuals, were not attempted. Analysis of the coverage data from each site allows calculation of average cover, relative cover, frequency, relative frequency and an importance value (rel. cover + rel. frequency) for each species encountered in the sampling.

During June (18-24) and July (20-22) 1984 further inventory work concentrated on locating more alvar sites, listing the plant species found there and assessing the degree of human disturbance. Sites sampled in 1983 were also checked at this time for species that were not previously recorded in the vegetation sampling. Voucher specimens for all species encountered in both 1983 and 1984 are deposited in the Michigan State University Herbarium (MSC).

2. Similarity of sites studied.

Similarity of sites can be calculated using species lists or by using a measure of species importance. A measure of community similarity that includes species importance is much more informative since differences in dominance are encompassed. The Shannon diversity index and Horn's index of community similarity (Brower and Zar, 1977) were calculated for the sites sampled in 1983. Horn's index was then used to construct a dendrogram representing these community similarity relationships. The species lists compiled in 1984 were used in calculating the Sorensen coefficient of community similarity (Brower and Zar, 1977) for these sites. Similarly, a dendrogram representing these relationships was also constructed. Though this is a less informative measure of community similarity, it is presented to show relationships among the sites not studied in the vegetation sampling. Calculation of these indices was facilitated by using BASIC programs designed to evaluate all combinations of site pairs.

The dendrograms were constructed manually by first linking the sites with the highest similarity values and then adding additional sites to these groups according to decreasing similarity values. When a new site is added to an existing group of linked sites (or when one group of linked sites is added to another group of sites) the similarity value between this new site (or group) and the existing group is calculated by averaging all of the similarity values from site pairs between the new site and the existing group. This procedure is similar to cluster analysis using averaged linkage for cluster formation.

3. Relationships between biogeographic groups.

Biogeographic affinity was established for each of the species encountered on the alvars. As was noted in an earlier section, the following categories were used in this classification: 1) midcontinental 2) northern and cordilleran 3) circumboreal 4) eastern and Great Lakes 5) widespread within North America 6) cosmopolitan and 7) introduced. See pages 47-50 for a listing of the species in each of these groups.

Relationships between biogeographic groups were investigated through a series of correlation calculations. Correlations were established between both the number of species in a site belonging to each biogeographic group and the cover of species in these groups as a means of investigating these relationships.

4. Relationships between species composition and size of site.

In a similar manner, relationships between various aspects of species composition and size of the site were investigated through correlation calculations. Of particular interest were relationships between number and cover of species and area of site.

Areas of the sites were calculated by first projecting aerial photograph transparencies (artificial color infrared photographs taken in 1977, obtained from the Michigan Department of Natural Resources, scale = 1:24,000) and tracing the outline of the sites studied. The degree of enlargement was calculated by also projecting a centimeter grid onto a piece of drawing paper. The area of the traced outline was then calculated using a planimeter. This area calculation was then converted to true area of the site by dividing by the enlargement factor and then multiplying by a constant (5700) to convert the photograph area to true area. Enlargement by use of the overhead projector was elected because the error associated with planimeter measurements decreases as size of the area measured increases.

Results and discussion.

1. Vegetation composition and variability between sites.

Analysis of the alvar vegetation in the eleven sites sampled provides much interesting information about the species encountered. Appendix D contains summaries of the vegetation analysis calculations for each site, presenting the following measures of species contribution to the community: percent cover, frequency of occurrence, relative cover, relative frequency, importance value (rel. cover + rel. frequency) and rank of importance. Table 6 presents a compilation of the percent cover values for all species in the sites, as well as the calculated Shannon diversity values.

From these two summaries it can be seen that there are major differences in composition and dominance between the three small sites, 34-2, 34-3 and 36-6 and the other, larger sites. Most notable is the presence and strong dominance of *Sporobolus heterolepis* in all but these three small sites. *Eleocharis compressa* shows a similar occurrence pattern but with lesser percent cover values. In the absence of the

Table 6 Percent cover of species in 11 sites as calculated from vegetation sampling in 1983.

	28/ 29-1	33-4	28/ 33-1	29-2	34-1	33-2	34-5	36/ 31-1	34-3	34-2	36-6
Achillea millefolium ssp. *lanulosa*	1.0	.4	2.5		.2	.3	.1	6.3	6.9	1.3	2.0
Agropyron trachycaulum	1.3	1.6	3.8	.1	.9	1.0	2.0	2.4	1.8		.6
Agrostis gigantea								.2	.6		
Ambrosia artemisiifolia	.3	.6	.3	1.1	.1						
Amelanchier sanguinea						.2	.2			1.0	2.0
Anemone canadensis									.4		
Apocynum androsaemifolium					.2		.7			1.2	
Arctostaphylos uva-ursi					3.4	1.6	1.1	2.3	15.1		
Arenaria serpyllifolia									.1	2.5	
Arenaria stricta	.1	.1			1.0		1.1	.4			
Artemisia campestris ssp. *caudata*					.9			.1			
Aster ciliolatus						.2		.1	2.3	1.1	
Aster pilosus var. *pringlei*		.4			1.3			4.5			.6
Aster ptarmicoides	.5	.6	.2		.1	.9	.6	1.2			
Botrichium simplex	.1		.2	.1							
Bromus kalmii	.3	.1	1.1	.1	.3	.7	.2		.6		
Campanula rotundifolia	.4	.3			.7	.3	.8	.7	1.8	1.3	
Carex crawei	1.7	1.4	1.0	1.4	.6	4.0					
Carex garberi	.4	1.6	.4								
Carex merritt-fernaldii			.2		.4			.5			
Carex richardsonii	.5		.5			1.3	.4				1.5
Carex scirpoidea					4.4	.7	8.1				
Carex umbellata	2.3	3.1	2.4	.7	.2	1.8	1.8	2.4	.7		.9
Castilleja coccinea	.1		.1		.1						
Cerastium arvense			.2	.7	.2		.4	4.2	.1		
Chrysanthemum leucanthemum								.7	4.0	3.3	6.8
Comandra umbellata		.2			1.0	1.3	1.2	.6	4.9	4.9	.1
Danthonia spicata	.4	1.8	.3	2.0	3.2	2.3	3.7	1.7	17.1	.2	1.0
Deschampsia cespitosa	.1	.9	.9		.6	.3	.1	1.9			
Dichanthelium accuminatum	.1		.1		.5						
Eleocharis compressa	18.8	16.9	10.3	22.3	5.4	4.6	.3	4.3			
Equisetum arvense					.1			.1			
Epilobium ciliatum		.1		.3							
Festuca ovina var. *saximontana*						.1					
Fragaria virginiana	.6	.9	6.0	.6	1.0	2.9	2.5	5.0	11.1	16.4	17.4
Geranium carolinianum	.2	.1	.1	.4						.4	
Geum triflorum	.3										
Hieracium aurantiacum		.1							4.5		
Hieracium piloselloides	2.3	1.9	3.4	1.8	1.7	1.5	5.1	7.3	12.2	8.1	8.3
Hypericum perforatum		.1	.6	1.5	.9	2.1	5.5	.1	.8	1.5	6.5
Juncus dudleyi	.2		.1	.1							
Juniperus communis	.4	1.4	.2	.4	.2	.9	.1				
Juniperus horizontalis					7.0		.2				
Lathyrus palustris	.1		.1			.1		.1			
Medicago lupulina									2.2	.6	
Phleum pratense	.5		1.6	.1	.1			6.2	3.1	7.0	3.1
Poa compressa	5.4	1.4	8.4	10.6	4.4	2.8	3.0	13.6	5.2	7.7	9.8
Poa pratensis	.4		.6					3.3	8.5	24.3	2.8
Populus tremuloides									.1		
Polygala senega				.1		.1					
Potentilla fruticosa					.2		.1				
Prunella vulgaris var. *lanceolata*				.2	.4	.3		.7	1.0	1.9	3.1
Prunus pumila var *depressa*					1.7		1.2				
Ranunculus fascicularis	.1	.1	.4	.8		.1	.1	.4			
Rhus aromatica					.4		.5				
Rosa acicularis		.4					.1	1.3		1.8	.2
Satureja vulgaris			.1		.1				1.3	.3	
Schizachyrium scoparium	4.1	1.7	1.3	.7	5.4	8.8	5.0				
Scutellaria parvula	.3	.3	.4	.9		.1	.1				
Senecio pauperculus	7.6	2.9	6.5	14.0	2.4	1.4	.9	11.7			6.8
Sisyrinchium montanum			.1	.1		.1		.1			
Smilacina stellata			.1					.2			
Solidago canadensis										4.2	
Solidago nemoralis					.2	.4					
Sporobolus heterolepis	36.7	33.7	42.8	46.9	18.1	25.7	23.6	21.0			
Symphoricarpos albus					.1		.6		.7	2.5	
Taraxacum officinale	.1	.1	.2	.2	.1			.1	.1	.5	.9
Tragopogon pratensis							.1				
Trifolium hybridum								3.5	2.6	15.8	
Veronica arvensis	.1			.1							
Zigadenus glaucus					.3			.4			
Shannon Diversity	2.03	2.00	2.18	1.82	2.84	2.44	2.52	2.83	2.73	2.53	2.43
Number of species	34	30	36	28	42	32	34	36	28	24	19

strong dominance of *S. heterolepis*, these smaller sites have higher cover contributions from *Fragaria virginiana*, *Hieracium piloselloides*, *Poa pratensis*, *Chrysanthemum leucanthemum* and several other species. These sites generally have a less pronounced dominance by one or a few species and, accordingly, their measure of diversity is higher. Several of the weedy introduced species are recorded, or have the greatest cover, in the vegetation analysis from these smaller sites.

Among the eight larger sites dominated by *Sporobolus heterolepis* there are several noteworthy patterns in the composition of these sites that can be seen in the cover values. Of the sites in which *Eleocharis compressa* was recorded, four of them have cover values for this species over 10% and four of them have cover values of 5% or less. The same pattern is seen in the cover values for *Sporobolus heterolepis*. The reverse of this pattern of cover values is seen in those values calculated for *Schizachyrium scoparium*, though less clearly because the differences are smaller and because the species was not recorded in one site (36/31-1). These patterns observed in the cover values may be due to differences in some feature(s) of the sites in question, such as soil moisture, soil depth and drainage characteristics. These parameters are especially suspect since *Eleocharis compressa* appears to be most strongly developed in the moister (though not in the extremely wet) microsites and *Schizachyrium scoparium* appears to be most strongly developed in the drier microsites.

From Appendix D it can be seen that among the eight larger sites, the following species tend to have the highest importance ranks: *Sporobolus heterolepis*, *Eleocharis compressa*, *Senecio pauperculus* and *Poa compressa*. The order varies from site to site with the exception that *Sporobolus heterolepis* is always ranked highest. Several species have high importance values not due to high relative cover estimates, but rather to high relative frequency values. This is true most notably of *Poa compressa* and *Hieracium piloselloides*.

There are also features of the alvar vegetation that are common to all of the sites sampled. For example, in the vegetation sampling the following species were frequent enough to be recorded in all sites: *Danthonia spicata*, *Fragaria virginiana*, *Hieracium piloselloides* and *Poa compressa*. Appendix E provides a listing of all the species encountered in the summer of 1984 for 29 sites. From this listing it is evident that there are other species that are found in nearly all of the alvar sites and the apparent absence of such widespread taxa as *Achillea millefolium*, *Hieracium piloselloides*, *Senecio pauperculus* and others from only a few alvar sites are likely cases of the species being present in the site but inadvertently not being recorded.

Measures of community diversity are calculated here in the form of the Shannon diversity index and are presented in Table 6. This measure of diversity encompasses both the number of species present and their importance in the community. Here importance is estimated through measures of percent cover. A community can have a higher diversity value than others it is being compared with by having either a larger number of species or by having a more even range of importance estimates (less dominance by a few species). The values calculated for the eleven sites sampled provide examples of this. Site number 34-1 has both the greatest number of species and the least dominance by Sporobolus heterolepis and consequently has the highest calculated diversity value.

An interesting comparison can be made between sites 34-3 and 29-2. Both of these sites have 28 species recorded in the vegetation analysis. Site 34-3 lacks Sporobolus heterolepis and has four codominant species with cover values ranging between 11.1 and 17.1 percent. The diversity value for site 34-3 is 2.73. Site 29-2 has Sporobolus heterolepis as the dominant species (highest cover value recorded in all sites, 46.9%), three species with cover values between 10.6 and 22.3 percent and only five species with cover values between 1.0 and 2.0 percent. In this site there are many species with cover values less than 1.0%. As a consequence of the strong dominance by Sporobolus heterolepis and the very limited importance of other species, the diversity of site 29-2 is only 1.82, the lowest calculated value.

Another interesting comparison is between sites 33-2 and 36-6. The diversity values for these sites are 2.44 and 2.43 respectively. The number of species recorded in these sites (32 and 19 respectively) and the degree of dominance are quite different. In this instance two sites with very similar diversity values are in fact quite different. Further investigation of similarities and differences between sites will be presented in the next section of this discussion.

2. Similarity of sites.

As a means of objectively examining the degree of similarity between sites, Horn's index and Sorensen's coefficient, both measures of community similarity, were calculated for all pairwise combinations of sites. As mentioned earlier, Horn's index uses the Shannon diversity index in estimating similarity between sites. Since this calculation encompasses differences in importance of species, the resulting value, Horn's index, is indicative of not only similarities in species composition, but also similarities in dominance. Sorensen's coefficient, however, only reflects similarities in composition. Use of this latter estimate of similarity was desirable since many of the sites surveyed in 1984 were not sampled in 1983 and appear to be of varying composition. Appendix G lists all similarity values calculated in the pairwise site comparisons mentioned above.

Diagrammatic representation of similarities between sites is provided by dendrograms which cluster similar sites and show averaged similarity between these groups. Figure 3

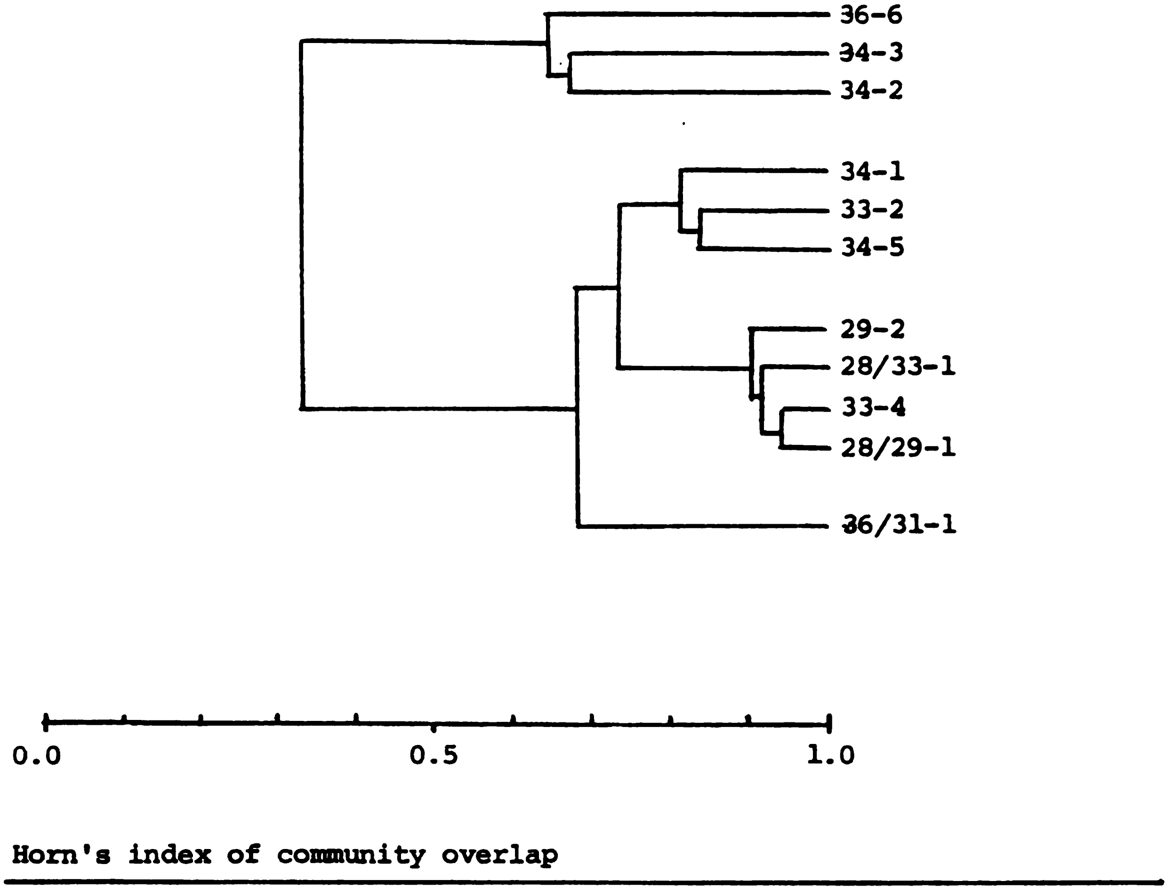


Figure 3 Similarity of communities sampled. This calculation of similarity is based on the Shannon diversity index and Horn's index of community overlap (Brower and Zar 1977).

presents similarity relationships between the eleven sites sampled in 1983. Several patterns are apparent from this diagram. The eleven sites can by broken down into four groups containing 3,3,4 and 1 sites in each. These four clusters are well defined and represent obvious differences in the communities that can be distinguished in the field.

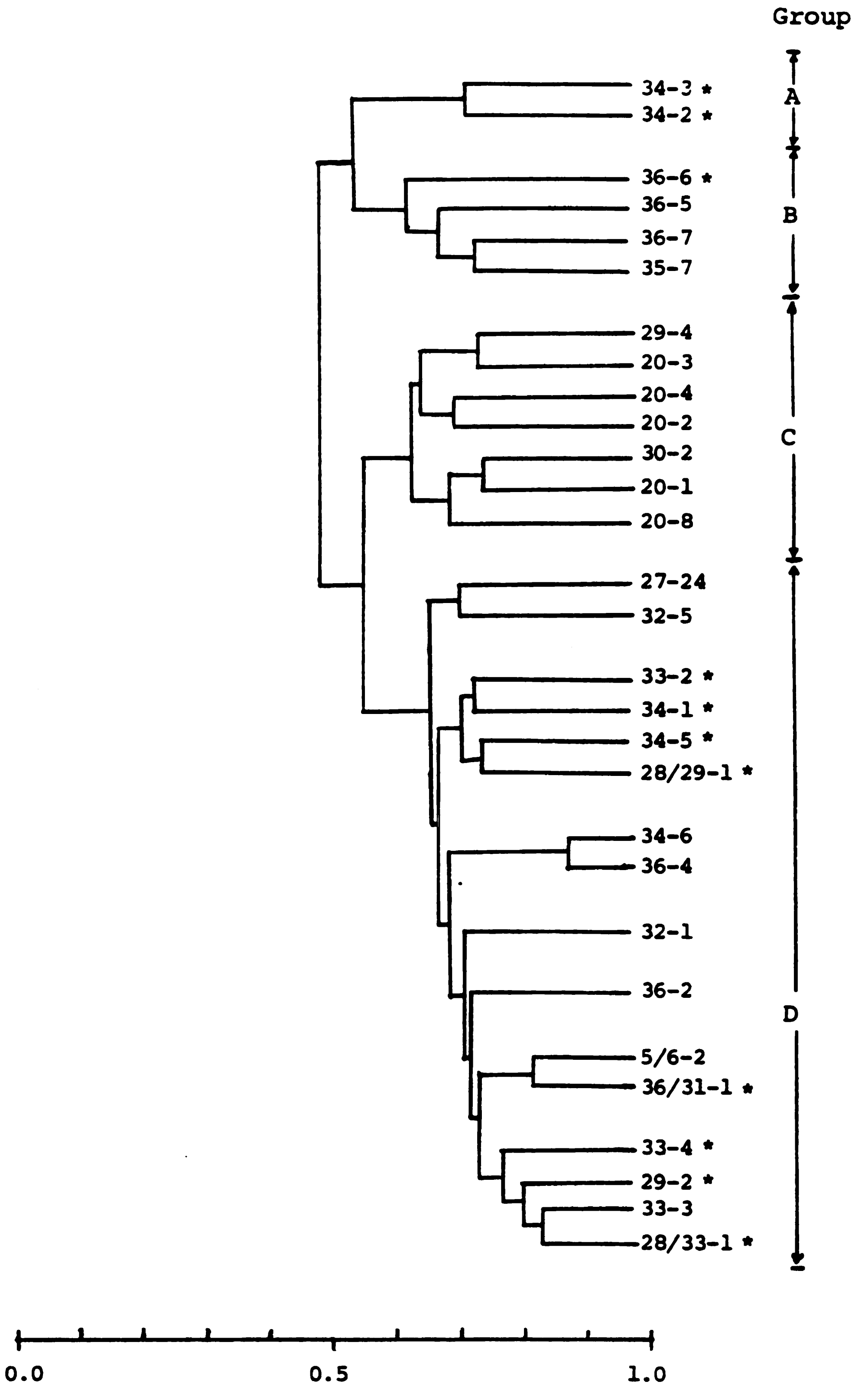
The first cluster, containing sites 36-6, 34-3 and 34-2, is the group of sites mentioned in the preceding section of this discussion which lacks Sporobolus heterolepis and supports a relatively large proportion of introduced weedy species. These sites are all relatively small (see figure 5 for size comparisons) and are all in close proximity to roads. Though this group is quite distinct from the remainder of the sites (average similarity value .33), similarity values among the three members are rather low (.67 and .64), especially when compared to similarity values among members of the other groups.

The cluster of sites containing 28/29-1, 33-4, 28/33-1 and 29-2 is also a well defined group. This group has quite high similarity values among its members. These sites have the greatest development of Sporobolus heterolepis and though their species numbers are close to the average number recorded in the vegetation analysis, their diversity values reflect this strong dominance in that they are the lowest calculated. Sites 34-5, 33-2 and 34-1 form the third cluster of similar sites. Dominance by Sporobolus heterolepis is not as strongly developed in these sites and cover values of subdominant species are generally higher than in the previous cluster. The two groups of sites just mentioned are both relatively free of strongly developed populations of introduced weedy species. These two clusters are joined at the 0.73 level to form a larger group of seven sites.

Although site 36/31-1 appears to be a distinct group, it is important to note that it is as similar to this group of seven sites as are the members of the group containing 34-2,34-3 and 36-6 to each other. The composition of site 36/31-1 can be recognized in the field as being distinct and this is due, as can be seen in Table 6, to a relatively larger number of species and smaller degree of dominance by Sporobolus heterolepis, rather evenly represented subordinant taxa and more well developed populations of introduced weedy species. Three such species are: Hieracium piloselloides, Phleum pratense and Trifolium hybridum. The greater representation of weedy species in site 36/31-1 suggests a greater degree of human disturbance in this site.

Figure 4 presents calculated similarity relationships among the 29 sites surveyed in 1984. In this figure relationships among sites that have been evaluated through Horn's index are marked with an asterisk. Several patterns are also evident in this figure. In this diagram there are again four major groups of sites discernible. It is interesting to compare the suggested relationships among the eleven sites examined in Figure 3 with the relationships suggested for the same sites in Figure 4. Assuming that

Figure 4 Similarity of communities as calculated using Sorensen's coefficient of similarity. This value is calculated using species presence as recorded in species lists and thus does not account for differences in importance of species. See text for discussion of group designations.



Sorensen coefficient of similarity

* Indicates a site that was sampled for vegetation analysis.
For relationships among these sites see Figure 3

Figure 4.

Figure 3 is a more accurate representation of community similarities, since it encompasses species importance, it is evident that the use of Sorensen's coefficient will not portray as accurately relationships among a number of relatively similar assemblages. In addition to changes in the composition of several clusters of sites, this lack of resolution is further evidenced by the generally close links between the subunits of group D. In both diagrams the three smaller sites, 34-2, 34-3 and 36-6, are distinguished from the others.

The ability of Figure 4 to portray more fundamental differences between species assemblages suggests that the major groupings of sites may be accurately represented. Group C is an excellent example of a group of sites obviously distinct from the others. These sites are all located on the northwest end of the Maxton Plains, are close to the shoreline and have especially shallow soil. Groups A and B both contain relatively small sites which lack Sporobolus heterolepis and which support a higher number of introduced weedy species. Group A contains sites located in the central part of the Maxton Plains and is clearly distinguished from group B, which contains sites located toward the eastern end of the Plains, a region which has been much more influenced by human activities.

These figures provide a good diagrammatic representation of the similarities and differences between the sites examined. They help to more clearly define several types of species assemblages and dominance patterns which are more or less evident in the field. Further examination of other relationships between groups of species will be presented in the following sections of this discussion.

3. Relationships between biogeographic groups.

Relationships between the species of the seven biogeographic groups defined earlier show several interesting patterns. Correlations between both the number of species recorded in a site belonging to the various biogeographic groups, and the total cover of species belonging to these groups show definite relationships between several of the biogeographic groups. Correlations utilized to examine relationships between number of species of a biogeographic group recorded in a site use data derived from the species lists prepared for 29 sites in 1984. Correlations utilized to examine these relationships using percent cover of species use data from the vegetation analysis of 1983. Table 7 presents listings of both, the number of species recorded in each site, and a summary of the cover of species in each site according to biogeographic group.

In the following presentation and discussion of these results it should be kept in mind that correlations cannot answer questions of cause and effect, and where explanations for certain relationships are suggested, the interpretations are not taken to be proven by significant correlation

Table 7 Number of species and percent cover of species by biogeographic group.

Site	Total	Introduced		Northern		Circumboreal		Widespread		Cosmopolitan		Midcontinental		Eastern	
5/6-2	40	8	.20	5	.12	9	.22	5	.12	0	.00	8	.20	5	.12
30-2	49	6	.12	6	12	12	.24	3	.06	2	.04	13	.26	7	.14
20-1	49	6	.12	5	.10	11	.22	8	.16	1	.02	11	.22	7	.14
20-2	25	5	.20	2	.08	4	.16	2	.08	1	.04	8	.32	3	.12
20-3	38	4	.10	6	.16	9	.24	4	.10	1	.03	10	.26	4	.10
20-4	30	3	.10	2	.07	7	.23	4	.13	0	.00	10	.33	4	.13
27-24	35	6	.17	1	.02	8	.23	8	.23	1	.03	7	.20	4	.11
28/29-1	80	17	.21	8	.10	13	.16	11	.14	4	.05	19	.24	8	.10
28/33-1	53	8	.15	4	.07	11	.21	6	.11	2	.04	16	.30	6	.11
29-2	40	9	.22	4	.10	9	.22	7	.18	1	.02	7	.18	3	.08
29-4	28	3	.11	3	.11	8	.28	4	.14	1	.04	8	.28	1	.04
32-1	37	7	.19	3	.08	7	.19	5	.14	1	.03	7	.19	7	.19
32-5	34	5	.15	4	.12	7	.20	7	.20	2	.06	8	.24	1	.03
33-2	45	6	.13	4	.09	7	.16	7	.16	3	.07	13	.29	5	.11
33-3	46	7	.15	4	.09	10	.22	7	.15	2	.04	10	.22	6	.13
33-4	38	7	.18	3	.08	8	.21	6	.16	1	.03	10	.26	3	.08
34-1	56	8	.14	5	.09	13	.23	8	.14	3	.05	12	.21	7	.12
34-5	61	11	.18	4	.06	14	.23	10	.16	1	.02	16	.26	5	.08
34-2	23	8	.35	3	.13	4	.17	4	.17	1	.04	2	.09	1	.04
34-3	25	9	.36	2	.08	6	.24	3	.12	1	.04	3	.12	1	.04
34-6	42	8	.19	4	.10	10	.24	5	.12	1	.02	10	.24	4	.10
35-7	48	9	.19	6	.12	7	.14	6	.12	2	.04	13	.27	5	.10
36/31-1	40	9	.22	4	.10	9	.22	5	.12	0	.00	8	.20	5	.12
36-2	50	11	.22	5	.10	9	.18	6	.12	3	.06	11	.22	5	.10
36-4	45	9	.20	5	.11	8	.18	7	.16	2	.04	9	.20	5	.11
36-5	36	10	.28	5	.14	7	.19	4	.11	0	.00	6	.17	4	.11
36-6	33	9	.27	4	.12	4	.12	5	.15	0	.00	7	.12	4	.12
36-7	32	5	.16	4	.12	5	.16	5	.16	0	.00	11	.34	2	.06
20-8	41	3	.07	5	.12	8	.20	6	.15	1	.02	10	.24	8	.20
Mean (number of species)	41.3	7.4		4.1		8.4		5.8		1.3		9.8		4.5	

Number of species and proportion of total by biogeographic group.

Site	Total	Introduced	Northern	Circumboreal	Widespread	Cosmopolitan	Midcontinental	Eastern
34-1	70.5	7.2	9.5	11.7	5.5	0.6	26.6	9.4
33-2	68.9	6.4	1.7	5.2	5.2	0.4	44.8	5.2
33-4	75.2	3.6	3.4	4.6	3.5	0.0	41.2	18.9
28/29-1	97.4	14.2	6.7	8.5	6.7	0.0	50.5	10.8
36/31-1	109.7	31.0	13.2	21.3	7.8	0.9	26.3	9.2
28/29-1	88.0	8.4	7.8	4.0	1.6	0.0	46.9	19.3
34-5	71.5	13.7	1.8	12.8	8.0	0.0	33.5	1.7
34-3	109.7	31.4	3.0	34.2	32.2	2.3	6.6	0.0
29-2	108.3	14.3	14.5	1.3	4.1	0.2	51.6	22.3
34-2	109.8	43.7	5.4	26.9	25.7	2.2	4.9	1.0
36-6	74.4	28.6	7.0	5.4	25.2	3.1	2.5	2.6
Mean	89.4	18.4	6.7	12.4	11.4	0.9	30.5	9.1

Percent cover of species by biogeographic group coefficients. It should also be recognized that changes in taxonomic interpretation of a species could significantly alter the interpretation of biogeographic affinity for the species and thus change the correlations calculated here. One of the primary assumptions of, and reasons for, an analysis of biogeographic patterns is that most of the species of each of these groups are assumed to share some life history characteristics which result in more or less similar distribution patterns. These assumed shared characteristics may also be implicated in the relationships between various biogeographic groups.

From Table 8 it can be seen that all relationships between the number of species in a site, grouped according to biogeographic affinity, are positive, and only four are not statistically significant. This result is not surprising and is interpreted to indicate that no one group of species has a dominating influence over another, with respect to number of species recorded.

What is surprising are the comparisons that yield nonsignificant values: midcontinental-introduced (.307), eastern/Great Lakes-introduced (.260) circumboreal-introduced (.361) and widespread-northern (.358). These nonsignificant correlation values are interpreted to indicate the following about factors that may be influencing the number of species occuring in a site: 1) different factors may be influencing the number of species of a biogeographic group occurring in a site 2) these relationsips are influenced by factors producing both

Table 8 Relationships between biogeographic groups of species as represented by number of species in each group occurring in a site.

Correlation matrix:

	Intro.	North.	Circu.	Wsprd.	Cosmo.	Mdctl.
Northern	.456*					
Circumboreal	.361	.505*				
Widespread	.467*	.358	.613*			
Cosmopolitan	.401*	.466*	.460*	.520*		
Midcontinental	.307	.579*	.694*	.584*	.568*	
Eastern/Grt Lk	.260	.559*	.618*	.440*	.394*	.610*

Critical value (2-tail, prob=.05) = ± .366

positive and negative effects, resulting in much variability. These factors can be separated into two groups. First, and probably most important, are those factors resulting in positive influences to both groups being compared, e.g., the capacity of a site to support more species increases with an increase in size. Second are the factors that would have a negative influence on one group and a positive influence on the other. Human disturbance, in the form of various activities, is one such factor that could have a negative influence on the species of some biogeographic groups, for example the native midcontinental and eastern/Great Lakes species, and a positive influence on species of other biogeographic groups, such as the introduced weedy species. That all of the correlation coefficient values calculated for these comparisons are positive suggests that the overriding influence is the capacity to support increasing numbers of species. The negative influences are most important to the midcontinental and eastern/Great Lakes species and though they are not strong enough to result in a negative correlation with the introduced species, they do result in an increase in variability of species representation such that the positive correlations are not significant.

Finally, it should be noted that though there are many significant relationships suggested, the correlation coefficients are rather low and thus they show that there is much unexplained variability in these relationships.

In many ways, the relationships between these biogeographic groups as examined by means of percent cover of species (arcsine transformed) are quite different. Table 9 presents the calculated correlation coefficients between these groups. From this table it can be seen that the cover of circumboreal, widespread and cosmopolitan species are all positively correlated with each other. The positive relationships can be interpreted as representing similar life history characteristics among the species. It is interesting to note that all significant correlations with the midcontinental group are negative, with the exception of the eastern/Great Lakes species. Likewise, all significant correlations with the group of eastern species are negative. These strong negative relationships could be interpreted as suggesting a dominating influence of the midcontinental and eastern/Great Lakes species over members of the other groups.

The strong positive relationship between the midcontinental and eastern/Great Lakes species is surprising since the reverse might be expected, given the strong dominance of members of both of these groups. This positive relationship could be explained in several ways, including: having similar competitive abilities with either microhabitat segregation or nonoverlapping phenologies. Of these, the differences in microhabitat utilization between *Eleocharis compressa* (eastern/Great Lakes) and *Sporobolus heterolepis* and *Schizachyrium scoparium* (midcontinental) are most obvious with *E. compressa* being most well developed in

Table 9. Relationships between biogeographic groups of species, and with area of the alvar site, as represented by correlations using percent cover of species.

Correlation matrix:

	Intro.	North.	Circu.	Wsprd.	Cosmo.	Mdctl.	East./ Grt Lk
Northern	.172						
Circumboreal	.703*	-.192					
Widespread	.824*	-.221	.688*				
Cosmopolitan	.770*	.078	.536	.863*			
Midcontinental	-.774*	.115	-.637*	-.922*	-.908*		
Eastern/Grt Lk	-.638*	.536	-.758*	-.857*	-.662*	.771*	
Area	-.449	.317	-.168	-.690*	-.646*	.656*	.461

Critical value (2 tail, prob=.05) = ± .600

Percent cover is arcsine transformed, area is square root transformed.

slight depressions and other moist situations, S. scoparium in the drier situations and S. heterolepis strongly developed on substrates that are intermediate along this moisture gradient.

The preceding discussion concentrated on relationships between groups of species occurring on the alvars. Further examination of patterns in the alvar vegetation focuses on relationships of size of the alvar sites with composition.

4. Relationships between species composition and size of alvar sites.

Table9 also presents the calculated correlation coefficients that address the relationships between size of alvar sites (log transformed) and percent cover (arcsine transformed) of the species of various biogeoraphic groups. From these values it can be seen that the cover of midcontinental species is positively correlated with area and that of widespread and cosmopolitan species are negatively correlated. Though these values are significant, it should benoted that they can account for only 43.0%, 47.6% and 41.7%, respectively, of the variation observed in these relationships. Much of the remaining variation is likely accounted for in the relationships between biogeographic groups. Considering these correlations and those discussed above (percent cover), it can be concluded that the dominance of midcontinental species generally increases with size of alvar site. This relationship is obscured somewhat due to the fact that several sites, of various sizes, are disturbed to some degree. Several reasonswhy this increasing dominance should be so can be offered. As the size of an alvar site increases, the ameliorating affects of the forest edge (primarily shade?) on such environmental parameters as insolation and evaporation are reduced relative to area. The result is that a large alvar should have more severe environmental conditions than a smaller site. It is the group of midcontinental species that should be most adequately adapted to these severe conditions of the large alvars and thus, show the strongest dominance in these sites. Also of probable importance is the fact that the small sites have been influenced to a greater degree by oscillating forest-grassland boundaries, with the result being that these areas are far less stable and thus, less suited to these species.

This pattern of increasing dominance of midcontinental species with size would be obscured if a subset of these species was reduced or eliminated from a site due to human disturbance. Disturbance, primarily in the form of grazing, appears to have been restricted to the eastern end of the Maxton Plains, mostly associated with lumbering activities around Scott's logging camp in the late 1800's (records from the museum at the village of Drummond). Sites 36/31-1 and 5/6-2 are the larger alvars in this area. That these sites have been disturbed is evident from the relative abundance of introduced weedy species and relative under representation of midcontinental taxa. Voigt and

Mohlenbrock (no date) note that both Sporobolus heterolepis and Schizachyrium scoparium decline under heavy grazing. In addition, it seems likely that the effects of grazing would be accentuated under the shallow soil conditions of the Maxton Plains, with the result that even moderate grazing could severely alter the grassland composition. Interpretation of the degree and consequences of disturbance is relatively obvious when comparing among the larger alvars. It is difficult to interpret the degree of disturbance in 34-2, 34-3 and 36-6, three small, rather weedy sites because of size differences between these sites and the large, undisturbed alvars of the west Maxton Plains. If both size of the alvar site as well as degree of disturbance are important in determining the representation of the midcontinental species, as they appear to be, then assessmentof disturbance should be based on comparisons of sites of approximately the same size. Unfortunately the only other sites in this size range that have been examined are on the northwest end of the Maxton Plains and appear to be rather different from the other alvar sites, as discussed earlier.

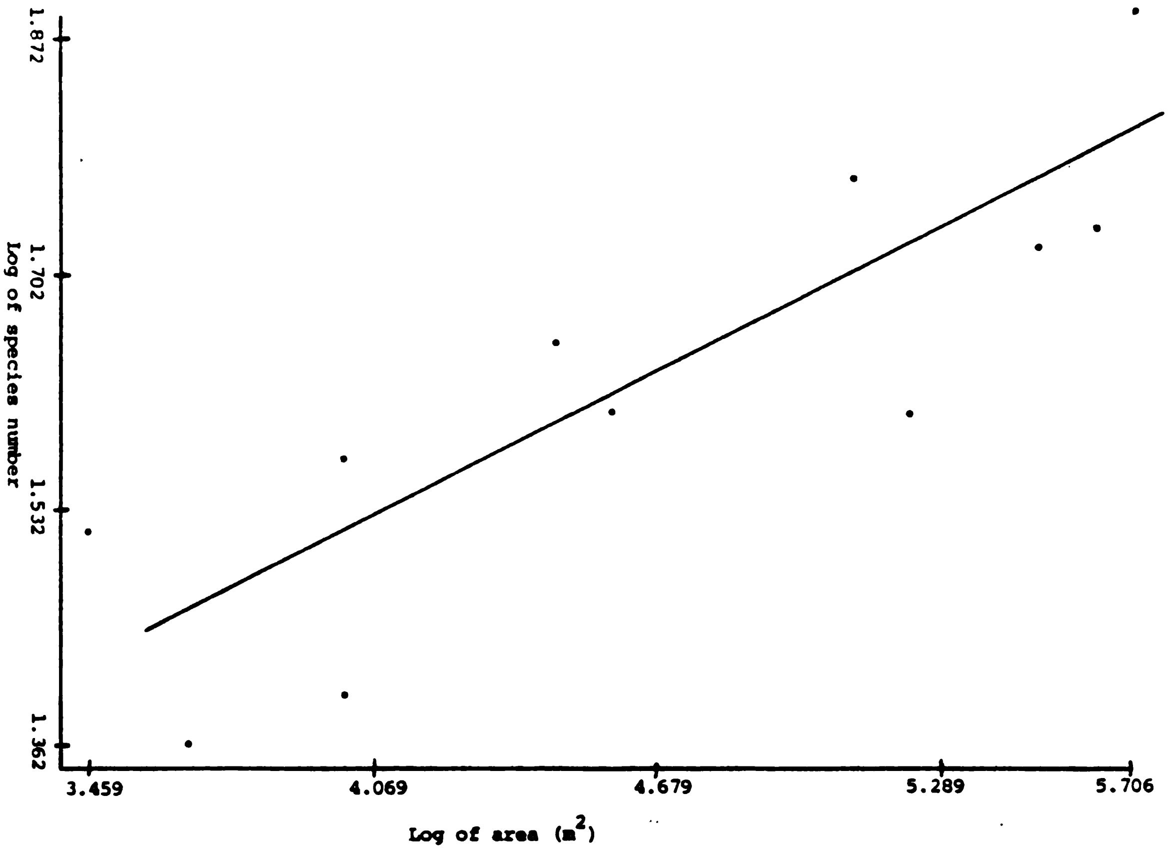
The fact that there is a negative but not statistically significant correlation (-.449) of the cover of introduced species with size of alvar site can be interpreted to suggest that sites of a relatively wide range of sizes have been disturbed (for example 34-3 and 36/31-1), thus introducing enough variability into this relationship as to result in a nonsignificant correlation value. The significant negative relationships indicated for the widespread and cosmopolitan groups of species are likely a result of the increasing severity of environmental conditions with increasing size of alvar site, as well as the superior competitive abilities of the midcontinental species under these conditions.

From this discussion it can be seen that alvar size is an important factor in determining the representation (cover) of species of various biogeographic groups. It can also be seen that because some sites have been disturbed much more than others, primarily through grazing, these relationships to size are somewhat obscured.

A final aspect of the flora that relates to size of alvar site is the relationship between number of species recorded in a site and its size. It is widely accepted that as the size of a community increases, the number of species recorded in the community increases. This positive species-area relationship is as applicable to community size as it is to sample size. This relationship is also quite important in investigations of island biogeography patterns. It is also of prime importance to conservationists when planning nature preserves (Wilcox, 1980; Simberloff and Gotelli, 1984).

The increase in number of species with size is often suggested to be primarily a function of increased habitat area and diversity (Wilcox 1980). When the log of community area is plotted against the log of species number the resulting relationship appears to be a linear function. Applying linear regression analysis to this relationship allows an estimation of the slope of this function, as well as a measure of the amount of variability not associated with the influence of size on species number. The slope of the line (regression coefficient) is interpreted as a measure of the vagility or dispersal abilities of the organisms being studied and of the degree of habitat insularity. Small regression coefficients (ca. 0.12-0.17) are taken to be indicative of samples rather than entire communitiesor "isolates", which tend to have values ranging between 0.18 and 0.35 (Wilcox, 1980). The slope would also be less if the isolates are closer togeather, less insular, or if the species have high vagility. In the case of the alvar sites, many of them are close together and only minimally separated.

Figure 5 represents the relationship between area and species content for the Maxton Plains alvars. From the r^2 value it can be seen that 71% of the variability is explained by this relationship. The slope of the line is estimated to be 0.170. It is suggested that this relatively low value for the slope reflects the fact that the alvar sites are quite close together and have a low degree of habitat insularity. It is possible that if the sites that have been disturbed are removed from this analysis and that if other sites can be added to increase the representation of the smaller sites, then perhaps a larger percentage of the variation can be accounted for in the analysis.



Site	Number Species	Area (m^2)	Log Species	Log Area
29-2	40	39398	1.60	4.46
34-1	56	400954	1.75	5.60
34-3	25	10368	1.40	4.02
36-6	33	2880	1.52	3.46
34-2	23	4608	1.36	3.66
28/33-1	53	310579	1.72	5.49
34-5	61	122688	1.79	5.09
36/31-1	40	169344	1.60	5.23
33-4	38	10080	1.58	4.00
33-2	45	27994	1.65	4.45
28/29-1	80	508378	1.90	5.71
Mean	41.6	45708	1.62	4.66

Regression coefficient= .170
T= 4.720
Prob.= .001

Analysis of variance
Regression F= 22.278
Prob.= .001

Figure 5 Relationship between area of alvar and number of species recorded.

SUMMARY.

The following conclusions can be summarized from the various aspects of the analysis of the alvar vegetation.

1. There are several basic associations or types of species assemblages on the alvars of the Maxton Plains. These are: a group of sites that appear to be distinct and associated with the northwest shoreline, a group of sites that appears to have been disturbed to varying degrees, and a group that appears to represent the bulk of the undisturbed, *Sporobolus heterolepis* dominated alvars. This latter group can be further divided, when examined for quantitative differences in species representation, into groups that may represent differences in environmental conditions, soil, moisture etc.

2. The midcontinental and eastern/Great Lakes species show a positive relationship with regard to percent cover and together they exhibit a pattern of dominance, suggested by negative correlations with the cover of species of the other biogeographic groups.

3. The midcontinental species exhibit a pattern of increasing dominance with increasing size of alvar site. This may be a result of one or several of the following factors: competitive abilities, adaptations to the comparitively harsher environmental conditions of the larger sites and, minimal influence of forest (from shading as well

as oscillations of the grassland-forest boundary) in the large sites.

4. There is a significant positive relationship between the size of an alvar community and the number of species recorded there. However, since the sites are minimally separated from each other,the relationship indicated more closely resembles that of increasing sample size than of increasing community size.

HISTORY OF THE ALVAR VEGETATION OF THE MAXTON PLAINS.

Introduction.

The history of the alvar vegetation has been examined through two different avenues of investigation. Aerial photographs from 1977 and 1939 have been used to map the extent of the open alvars at these time periods. Comparisons between these maps allow graphic representation of zones of vegetation changes which have occurred in the intervening years. The study of opal phytolith (plant silica) deposits in the soils reveal different aspects of the vegetation history.

Since opal is usually quite stable in soil deposits, its presence can be used as a tool in paleoecological studies of a much greater time span than is allowed with aerial photographs. Phytolith deposits also allow the study of changes in composition and dominance within the alvar sites. Specifically, the questions being addressed through the study of opal phytolith deposits are: 1) is there evidence of dominance by *Sporobolus heterolepis* and *Schizachyrium scoparium* in the alvar sites that presently lack dominance by these species, 2) is there evidence for influence of *Sporobolus heterolepis* and *Schizachyrium scoparium* in the transition zones and in adjacent forested areas.

In presenting the results of the opal phytolith analysis, ternary diagrams, as developed by Dr. Ralph E. Taggart for palynological studies, are employed here to more clearly illustrate the evidence for vegetation changes. The ternary diagrams fill a gap that has existed in the phytolith literature with respect to a method of clearly representing phytolith data such that any patterns, of vegetation change or otherwise, are evident.

Vegetation history as studied through aerial photographs.

Methods.

Aerial photographs taken in 1939 and 1977 were used to construct maps representing the vegetation of the Maxton Plains during those years. The aerial photographs taken in 1977 are artificial color, infrared transparencies and were obtained through the Michigan Department of Natural Resources. Open alvars can easily be distinguished from forested areas in these transparencies, though occasionally the hydrology of the alvar (i.e., "upland" and dry vs. low and wet) is difficult to determine. Since the transparencies are of the same scale as 7 1/2 minute topographic maps, vegetation boundaries were copied directly from the photographs onto tracing paper using a light table. Tracings were made from overlapping photographs, then assembled, adjusting for differences due to parallax, into a single map of the vegetation. This map was checked in the field for accuracy of interpretation during the field seasons of 1983 and 1984.

Black and white aerial photographs taken in 1939, obtained through the Center for Remote Sensing at Michigan State University, were utilized to represent the extent of the alvars in 1939. These photographs were reduced to conform to the scale of the 1977 transparencies. This was done using a reflecting projector available at the remote sensing lab.

The alvars on the 1977 map are indicated on Figure 6 by a stippled pattern and the area covered with forest vegetation is unmarked. The forested areas shown on the 1939 map are indicated by a solid shading on Figure 6 and the alvars remain unmarked. When these maps are superimposed, the unmarked portions of the map represent zones where forest has encroached onto the alvars. On this map such changes in the vegetation boundaries for the past 38 years can be observed.

Results and discussion.

Use of aerial photographs in studying the history of the alvars shows several areas of significant changes in the alvar-forest boundary. Though this approach does show some areas of vegetation changes, several shortcomings of the method should first be addressed. Of major significance here is the error in constructing the individual maps that is due to parallax differences resulting from different flight paths and positions when the photographs were taken. This is especially a problem when each map is composed of a composite of several individual photographs. An additional source of error involves judgement of the position of the boundary between forest and alvar. In most instances the boundary is very clear. Occasionally, however, it is not clear and an arbitrary decision must be made as to the position of the boundary.

Figure 6 represents the superimposition of the 1977 and 1939 maps and therefore a record of some of the vegetation changes that have occurred in the past 38 years. From this figure it can be seen that changes in the alvar-forest boundary have occurred in nearly every section that contains alvar sites. Some of the more pronounced changes can be seen in Sections 30 (by Bruce and Chippewa Points), 33, 34, 27 and 36 (T43N, R6E) of the central and west Maxton Plains and Sections 32 and 29 (T43N, R7E) of the eastern Plains. Only a few of the changes are associated with the southern edges of the alvars. These are generally quite stable, geologically controlled, community boundaries, being defined by abrupt ledges of one to several meters in height. In fact, many of the changes shown on Figure 6 for the southern boundaries of the alvars may be the result of parallax errors.

The sites in Section 33 south of site 28/33-1 (sites 33-3, 33-4, 33-2 etc.) show significant changes that are likely not the result of errors associatedwith parallax differences or differences in judgement of position of the

Figure 6 Map of the Maxton Plains representing changes in vegetation boundaries that have taken place between 1939 and 1977.


Chippewa Point
Grand Marias Lake
Dawson Lake
Bruce Point
Raynolds Point
Colton Bay
30
29
28
27
26
25
30
29
31
32
33
34
35
36
31
32
3
2
1
6
5
Alvars in 1977
Forest in 1939
Areas that forest has colonized since 1939
Miles
0
.5
1.0

gra
tha
irr
sur
197
Pop
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grassland-forest boundary. From this diagram it can be seen that these sites were all interconnected, forming one large irregularly shaped alvar in 1939. Much of the area surrounding these sites that is shown to be forested on the 1977 photos now consists of stands of young Picea glauca and Populus tremuloides. Similarly, the zones of significant change in Section 34 are associated with stands of relatively young aspen and spruce. Throughout all the alvars of the west Maxton Plains it can be seen that isolated "islands" of trees have grown in size since 1939, though most of them were present at that time, some only as small stands. It is likely that these tree islands will slowly grow in size until they are reduced or culled through drought or fire.

The changes that are represented in Section 27 appear to be significant but no information can be provided as to the nature of these changes at this time. From the aerial photographs those open areas appear to be identical to the other alvars and it is assumed that similar invasion patterns are taking place there.

Several of the alvar sites on the east Maxton Plains also show signs of recent vegetation changes. Portions of the east, north and west edges of site 36/31-1 appear to have changed. A more pronounced movement of the alvar-forest is evident along the shoreline in Sections 29 and 32 near Raynold's Point. No additional information can be provided concerning the nature of these changes.

Evidence of opening of a forested area is seen in site 28-12. This site is located south of Grand Marias Lake and can be seen as a distinct open area on the 1977 photographs and in Figure 17, Appendix A. Close inspection shows that portions of this site are wet, suggesting that the forest in this area was drowned sometime after 1939. Similarly, site 26-3 on the west end of Dawson Lake has been formed since 1939 through a local rise in the water level. It is possible that the activities of beaver in this area have altered the drainage pattern such that local flooding has resulted.

From this discussion it can be seen that some changes in vegetation boundaries are evident and that they represent significant colonization, primarily by aspen and spruce. It is also noted that minor movements of the alvar-forest boundary would be difficult to recognize because slight differences between maps can also be a result of the sources of error associated with this approach. This means that only relatively major changes that result in a different position and configuration of the boundary will be interpreted unambiguously.

Utility of opal phytoliths in paleoecological studies: a literature review.

Introduction.

In this section I will briefly review the nature of opal phytoliths and their utility in various kinds of biological studies. The phytolith literature that pertains to paleoecological studies will then be presented. This review of the literature will focus on those studies that have used opal phytolithsas tools inanalyzing vegetation changes. Recent papers that review other aspects of opal phytoliths will be mentioned only where appropriate.

Deposits of opal phytoliths can provide information regarding the nature of the alvar vegetation, with respect to the degree of influence of grasses in the community and the relative importance of various groups of grass species. In addition, the degree of importance of an aquatic component (algal) in the soil can also be evaluated.

Nature of opal phytoliths and phytolith deposits.

Opal phytoliths are silica deposits that accumulate in the tissues of many vascular plants. These mineral deposits are the same chemically as gem opal ($SiO_2 \cdot H_2O$) and are noncrystalline in nature (Seiver and Scott, 1963). The specific gravity of opal is 1.410 to 1.465. These and other minerological and chemical properties of plant opal were reviewed by Jones and Beavers (1963).

Because opal phytoliths have been used by researchers in a variety of disciplines, the terminology encountered in the literature can be quite variable. In anatomical and taxonomic studies, the term silica bodies is most often used. In soil science, the term plant opal is used. In the fields of archaeology, paleobotany and paleoecology, the preferred term for these structures is opal phytoliths. Accordingly, my use of terminology varies with the context of the study in question. As mentioned above, opal refers to the chemical composition and phytolith indicates that these structures are deposited as solid mineral material in plant tissues.

Baker (1959a) distinguished several types of silicified plant structures: 1) complete or nearly complete filling of various cells forming solid internal cell casts 2) thin and fragile silicification of internal cell linings forming fragile plate-like, sometimes ribbed fragments 3) complete cell wall replacements 4) silicified epidermal structures (hairs, hooks, spines and trichomes) 5) miscellaneous adventitious particles not conforming to organic structures. Of these types of opal structures, cell fillings are the most useful as paleoecological tools. Kaufman, Bigelow et al. (1971) and Kaufman, Dayanandan *et al*. (1984) have described patterns of deposition of silica in plant tissues and have hypothesized some structural and physiological uses of silica in plants.

Plants obtain silica through their water supply in the form of dissolved monosilicic acid. As water is used by the plant or lost in transpiration, excess silica is deposited in the tissues of the plant. The concentration of silica in plant tissues is dependent on several factors, including: silica solubility in the soil, soil temperature, moisture regime and nutrient status, transpiration rates and water use efficiency of the plant. It is not surprising that there can be much variability in the concentrations of silica in individuals of one species when grown in different soils. Jones and Handreck (1967) have reviewed aspects of the silica cycle in detail.

Dead plant material is usually deposited near its area of origin. As plant tissues decompose silica and other mineral deposits are released to the soil. Fragile siliceous deposits of the cell linings and cell wall replacements will often be fragmented as they become incorporated into the soil and thus, may be major sources of the fine, particulate component of opal deposits in soils. More resistant structures, such as cell infillings, hooks, spines etc. will often accumulate to significant amounts in the soil with minimal degradation.

Phytoliths are useful paleoecologically because of their mode of origin, patterns of deposition in the sediments, and their durability. In some groups of plants, notably the grasses, phytoliths of taxonomically distinctive morphologies are produced in large quantities. Jones and Beavers (1964a) note that the abundance of opal deposition in soils appears to be closely related to internal soil drainage, with soils in the middle drainage sequence (imperfectly drained to moderately well drained) having the higher opal contents. They also suggested that this is most likely due to differences in productivity, with soils of the intermediate drainage classes having the greatest potential for dry matter production though differences in silicate weathering potential are also important and can vary between drainage classes.

Jones and Beavers (1964a) also noted that they had no evidence of transport of opal materials into low, poorly drained areas from the surrounding uplands. This suggests that opal phytolith deposits may be expected to represent quite local sources and microhabitats. Opal phytolith deposits can be expected to be much more representitive of local situations than some deposits of pollen and spores since many pollen and spores are subject to broader dispersal. Opal phytoliths are probably at least as representitive of the local environment as are macrofossil deposits but not as easily differentiated to lower taxanomic levels.

Opal phytoliths are durable and can be preserved for long periods of time. Baker (1960) and Jones (1964) have reported dispersed phytoliths from fossil deposits dating to the Paleocene. Opal phytoliths can also be preserved in intact leaf fossils and were found in grass fossils from rocks of the late Miocene (Thomasson, 1980a; 1980b). Soil scientists have used deposits of fossil opal phytoliths as an "index mineral" as evidence for the existence of paleosols (Beavers and Stephen, 1958; Twiss et al., 1969). In addition to phytoliths occurring in some Tertiary deposits, Quaternary paleosols and modern soils, they are also reported to have been isolated from rainwater, tapwater and dusts (Baker, 1959a; 1959b; 1960b; Folger et al., 1967; Twiss et al., 1969).

Finney and Farnham (1968) demonstrated that aerial transport can be a significant source of opal input to a system in their study of the minerology of peat deposits from northern Minnesota. They found most of the opal was produced by grasses that do not grow in the bogs and they believe that it has been blown in as part of the dust from prairie regions to the west. The abundance of wind transported opal in a soil is a function of the direction and velocity of the prevailing winds and the proximity of a source.

Since opal phytoliths accumulate in soils as plant material is deposited and decomposes, the feasibility of stratigraphic applications has often been discussed. Geis and Jones (1973) note that the necessity of a stable, nonerosive soil surface for representation of vegetation changes may preclude stratigraphic applications in some instances. Also in question is the degree to which phytoliths may be eluviated to lower soil horizons. Rovner (1983) suggested that downward transport of opal phytoliths may not be a significant factor under normal circumstances. Most of the taxonomically distinctive phytoliths are siltsized particles and the eluviation of these materials is less likely than is the transport of the clay-sized, particulate opal materials. Soils that were or are subject to wind or water erosion would not be likely situations for stratigraphic applications.

Occurrence of opal phytoliths in plants.

Silica deposits, cell infillings, cell wall replacements, plates etc., are known to occur in many different groups of plants and with many different morphologies. The wood of many tree species is known to contain quite abundant deposits of silica. Rovner (1971) reports that opal materials were recovered from tissues of *Larix*, *Picea glauca*, *Juniperus virginiana* and *Pinus strobus*, with distinctive types from *Larix* and *Picea glauca*. *Equisetum* species are commonly known to contain abundant quantities of silica and these deposits have been shown to bemorphologically distinctive structures (Witty and Knox, 1964; Kaufman, Bigelow *et al*., 1971).

Among the Angiosperms, opal phytoliths have been reported from many families, including: Agavaceae, Asteraceae, Arecaceae, Cannaceae, Cyperaceae, Fabaceae, Juncaceae, Lamiaceae, Lilaceae, Plantaginaceae, Poaceae, Podostemaceae, Polygonacee, Restoniaceae, Scrophulariaceae, Thurinaceae, Verbenaceae and others (Rovner, 1971; 1983; Metcalfe, 1960; 1971). Recent interest in the occurrence and taxonomic differentiation of opal deposits has spurred survey work with the result that records of silica deposits in plants are becoming much more extensive. Many groups of plants, however, have yet to be examined and reports of taxonomically distinctive morphologies must be viewied with this in mind.

It is generally believed that the monocots produce opal phytoliths in significantly more abundant quantities than the dicots, as well as with taxonomically more significant variation. Monocots, and in particular the grasses, have received the most attention with regard to taxonomic differentation of phytolith morphologies, primarily because of the importance of members of the family as food and shelter sources. In fact, archaeologists have been primary contributors to the present understanding of phytolith differentiation.

Differentiation of opal phytoliths in the Poaceae.

Silica deposits, in the form of cell infillings are reported to occur in the epidermis of nearly every organ of the grass plant, including leaves, culm, roots and anthoecia. In grass leaves the epidermal cells can be divided into two major types: long cells and short cells. The short cells can be further classified as either cork cells or silica cells. Though silica deposits occur in both long cells and short cells, the deposits in the silica cell of the short cell-type are the most taxonomically distinctive. Patterns of the epidermis, including silica cell shape and phytolith morphology, are often used in systematic treatments to help in distinguishing subfamilial relationships (Metcalfe 1960, Stebbins and Crampton, 1961; Gould and Shaw, 1983). Metcalfe (1960) notes that of the vegetative organs of the grasses the most important diagnostic characteristics are to be found in the leaf. However, he cautions that there can be anatomical variability both within a leaf and between leaves of different levels on the plant. Metcalfe also notes that silica bodies from silica cells situated above vascular bundles (costal areas) tend to be more important taxonomically than are the silica bodies from intercostal areas.

Metcalfe (1960) divides the grasses into three groups, based largely on epidermal patterns. These groups are represented by the bambusoid, festucoid and panicoid types. He then subdivides the festucoid and panicoid groups into several tribes. It should be noted that the term pooid is synonymous with festucoid and its use (pooid) is more appropriate since Pooideae is the correct name of the subfamily to which grasses of this type belong. It should also be noted that in different treatments of the grass family some tribes are assigned to different subfamilies, with the result being that classifications of phytolith morphologies are in some instances more congruent with the family treatment than in others. Following is a summary of the silica body characteristics of the pooid (festucoid) and paniciod grasses as outlined by Metcalfe (1960).

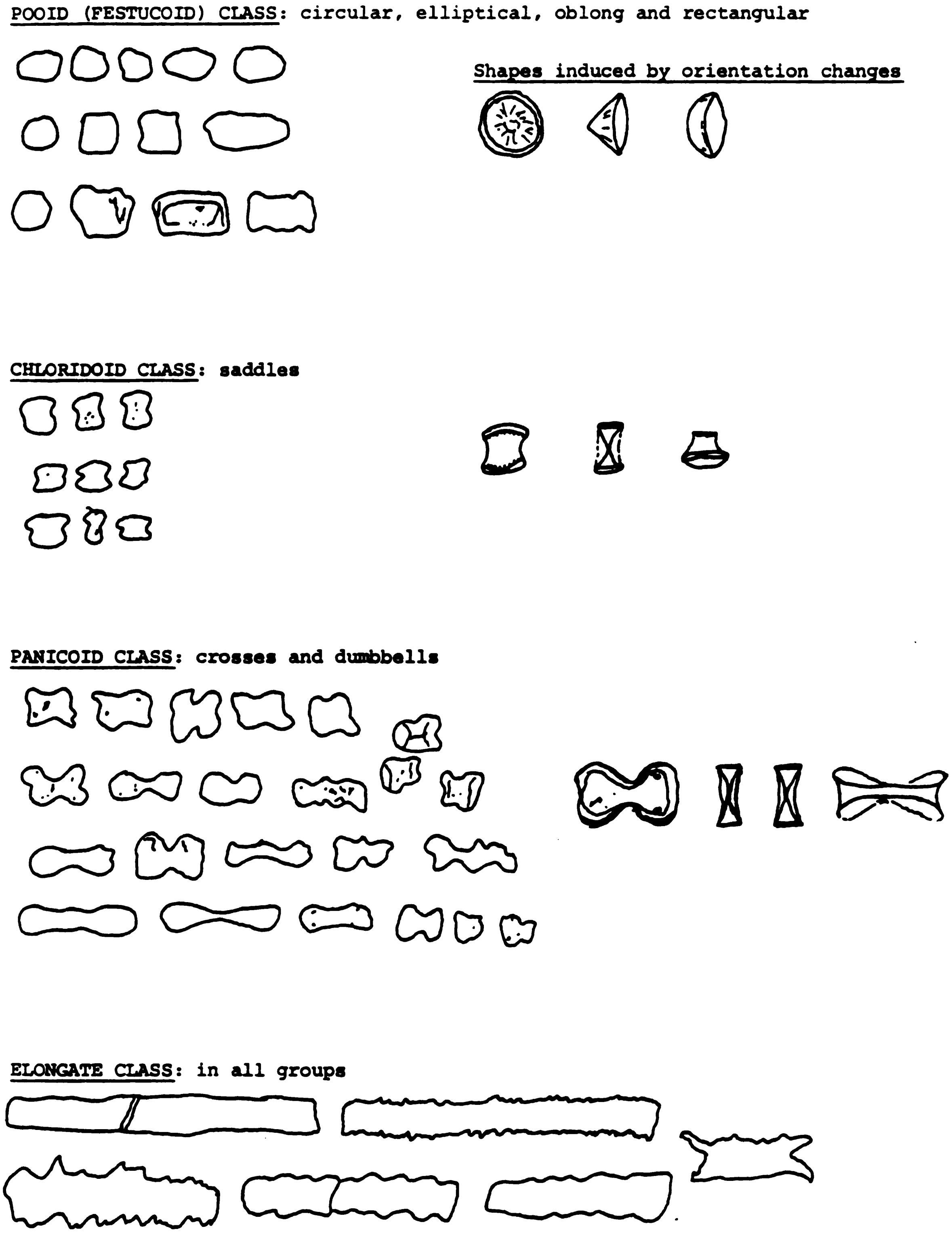
Pooid characters- Short cells over the veins are usually solitary or paired, seldom, if ever in longer rows. Silica bodies of one or more of the following types: tall and narrow, round, elliptical or crescent shaped and oblong.

Panicoid characters- Short cells over the veins are seldom solitary or paired, usually in rows. Silica bodies over the veins are saddle-shaped, cross-shaped, dumbbell-shaped and oryzoid or nodular-shaped. Intermediate types also occur. Included within this group are the following tribes: Andropogoneae and Paniceae with cross and dumbbell-shaped silica bodies, Maydeae with more frequently cross-shaped silica bodies, Chlorideae, Eragrosteae and Sporoboleae with a combination of pooid and panicoid features but primarily containing saddle-shaped silica bodies, and Danthonieae, a group that is not anatomically homogeneous with some pooid and some panicoid features.

Twiss et al. (1969) proposed a classification system for phytolith morphologies that recognized many of the distinctions outlined by Metcalfe (1960). In this classification system there are the following four morphology classes: pooid (festucoid), chloridoid, panicoid, and elongate. The saddle-shaped morphologies occurring in the Chlorideae, Eragrosteae and Sporoboleae were recognized as being distinctive morphologically and taxonomically and thus were worthy of being given equal rank with the other morphological classes. The elongate class, derived from silicified long cells, was noted to occur in all species examined and thus was not expected to be of much utility taxonomically. This classification system has been extensively used in most studies where phytolith identification was attempted. Diagramatic representation of the morphology classes designated by Twiss *et al*. (1969) is provided in Figure 7.

There are a number of limitations to the use of phytoliths that relate to differentiation of morphological types. Of prime importance is the fact that within a given species, in fact within a given individual, there are several shapes of phytoliths present, few of which appear to be unique to the species. This polymorphic condition is in contrast to that which occurs in pollen and spores,where a single repetitive form is characteristic, though the form may not necessarily be unique to a single species. Possible remedies tothe problem of polymorphic phytolith content involve assembling morphological "type assemblages" or suites of morphologies that are found in a given species (Rovner , 1971) or by establishing unique three dimensional characteristics that can differentiate phytoliths of different species, as has been done by Piperno (1984) with the phytoliths of maize and other grasses. One additional limitation of phytolith utility that should be mentioned involves differences in perceived shape as the orientation of the phytolith being viewed is changed. This problem was mentioned by Twiss et al. (1969) as was the fact that it could significantly affect an observer's abilityto assign the grain to a specific morphological type.

There are a number of reasons why recognition of



Redrawn from Twiss et al. (1969) and Metcalfe (1960).

Figure 7 Opal phytolith morphology classes as defined by Twiss et al. (1969).

taxonomic affinity of phytoliths is desirable. Grass pollen provides very little information with regard to taxonomic relationships within the family. Therefore, in palynological studies very little can be interpreted regarding the type of grassland community that might be represented in the pollen record. In addition, there are relatively few depositional environments in grassland communities in which preservation of pollen is possible. Opal phytoliths, however, have been shown to be taxonomically distinctive within the family and quite durable in many sediments. They are, therefore, potentially useful paleoecologically. There are great ecological, climatic and floristic differences between grassland communities of the various regions of North America (Teeri and Stowe, 1976) and it would be of great benefit to be able to distinguish these differences on the basis of opal phytolith assemblages in the soils.

There has been some interest lately in developing the ability to distinguish photosynthetic pathway (C_3 vs. C_4) on the basis of opal phytolith characteristics. Photosynthetic pathway is an important aspect of the ecology of grasses and is therefore of interest in paleoecological investigations. Rovner (1983) reviews methods of determining the photosynthetic pathway that involve measuring $^{13}C/^{12}C$ ratios of occluded carbon contained in phytoliths and $^{18}O/^{16}O$ ratios using the opal material itself. It should also be possible to determine photosynthetic pathway, in many cases, based on phytolith morphology since many of the subfamilies are represented by taxa that are all either C_3 or C_4. For example, the Pooideae is all C_3 and the Eragrostoideae is entirely C_4. The Panicoideae, however, contains both C_3 and C_4 members and would thus present difficulties in interpretation. A phytolith assemblage that is clearly dominated by pooid-type phytoliths (Pooideae- C_3) would clearly be indicative of different environmental conditions than would an assemblage dominated by chloridoid-type phytoliths (Eragrostoideae- C_4).

Paleoecological uses of opal phytolith deposits.

Various methods for extracting opal deposits from plant material, as well as soils have been outlined in numerous papers. Of these, the more standard procedures are presented in Twiss et al. (1969) and Rovner (1971, 1983). In addition, various other aspects of opal phytolith studies that are extraneous to the discussion here, particularly archaeological aspects, are reviewed by Rovner (1983).

Paleoecological studies that have utilized opal phytolith deposits as a tool in the investigation can be divided into two types of approaches. In one approach, phytoliths are isolated from the soils and total opal content of the soil, usually expressed as a proportion of the dry weight of either the whole soil or of a specific particle size fraction, is reported. In this type of investigation the characteristic total opal content of the soil is first established for a given set of communities. Changes in vegetation are then investigated through a subsequent comparison of total opal content between a number of soils some of which are believed to be supporting two stable communities, for example both grassland and forest vegetation, as well as with other soils which are hypothesized to be in regions of changing vegetation boundaries. Examples of this kind of strictly quantitative study of opal phytolith deposits are relatively numerous. Several of these will be summarized to illustrate the types of studies that have been undertaken.

Jones and Beavers (1964b) examined the variation of opal phytolith content in several soil groups in Illinois. They found similarities between soils developed under grassland and forest vegetation. In this study they compared soils of similar internal drainage characteristics, as they had suggested was necessary in another paper (Jones and Beavers, 1964a),and found that there was no significant difference between sets of Brunizem (grassland) and Gray-Brown Podzolic (fo and found that there was no significant difference between sets of Brunizem (grassland) and Gray-Brown Podzolic (forest) soils. Since it is expected that there would be a great difference between these soils, based on differences in production of opal material between grassland and forest, they conclude that the most obvious explanation is that forest recently expanded into the area that it now occupies in western Illinois and that the opal in these soils is a relict feature from grassland vegetation of the earlier Hypsithermal prairie expansion.

Witty and Knox (1964) investigated the stability of a grassland-forest boundary and the influence of a prior grassland vegetation on the soil in northcentral Oregon. In their study area they had clearly definable boundaries between vegetation types with uniform soil conditions. They found that some segments of the boundary have persisted in place for perhaps several thousand years while other localities show evidence of either invasion of forest into the grasslands or shrinking of forested areas and expansion of grassland. They also conclude that the present forest soils (i.e., away from zones of oscillation) have little or no history of grassland cover within the time span of persistence of grass opal. They note that data on actual rates of production and destruction of opal are needed before some meaningful interpretations can be made. Indeed, to this date very little additional information is available that can address these problems.

Jones, McKenzie and Beavers (1964) studied opal phytolith deposits in Michigan soils. Quantitative analysis of phytolith content was useful as an indicator of the extent of grassland occupation of a given site. In addition, they reportedevidence of a rather rich aquatic flora and fauna in the surface horizons of several soils. They illustrated siliceous resting structures belonging to members of the algal family Chrysostomataceae, diatom valves and sponge spicules. They attributed these deposits in some instances to aeolian transport and in other cases to changes in ecology of the sites. Based on my experience with the opal deposits on the Maxton Plains, which include these same opaline structures, I suggest that it is possible that many of these algal remains could represent soil inhabiting organisms that are able to flourish during seasonal periods of high water, as opposed to a planktonic flora and fauna Jones, McKenzie and Beavers (1964) have proposed for some sites.

Wilding and Drees (1968) studied opal phytolith deposits in several prairie-influenced and forested soils in Ohio with the objective of determining the total impact of prairie vegetation on the soils of the Prairie Peninsula region of Ohio. In this quantitative study they found that the total influence of prairie on the Gray-Brown Podzolic soils (forest) is about the same as it is on the Brinuzem soils (prairie). They concluded that either opalphytolith content is not a reliable index of grassland vegetation history, or forests have occupied the greater portion of the postglacial period with only recent periods of grass encroachment. Given the palynological evidence of minor prairie influence in Ohio and the other reports of reliability of opal deposits, they concluded that the latter mentioned explanation is the more likely.

A second major type of study or approach to using opal phytoliths involves attempts at determining subfamilial affinity of the plants that produced the phytoliths and then evaluating composition or composition changes within the grassland. Varma and Rust (1969) examined opal phytolith deposits in soils in southern Minnesota. They postulated that one soil type developed under dominant grassland vegetation because of the presence of high proportions of opal identical to material from _Andropogon gerardii_ and _Schizachyrium scoparium_. Another grassland soil was suggested to have had some influence of forest vegetation because of the presence of opal similar to that isolated from burr oak, ironwood and witch hazel.

Blackman (1971) observed opal phytoliths in the range grasses of southern Alberta and, though it was not a paleoecological study, made several observations that are pertinent to paleoecological applications. She noted that the use of phytoliths in a qualitative way to determine the species that once grew in a particular soil depends on a preliminary survey of the grasses concerned and on the establishment of good characters for identification and taxonomy.

Twiss (1983) reported on attempts to determine photosynthetic pathway of grass taxa as represented by opal phytolith morphologies. In a survey of the morphologies of silica bodies of various grass species, he noted that, of the taxa he examined, all of the species that produced festucoid class phytoliths (all in subfamily Pooideae) are C_3 grasses, all of the species that produced chloridoid class morphologies (all subfamily Erigrostoideae) are C_4 species and that all of the species producing the panicoid class of phytoliths (all Panicoideae) are C_4 species. He therefore suggests that these morphology classes can be used to determine photosynthetic pathway. There should not be much trouble with this assumption with regard to the festucoid and chloridoid morphology types. There is a problem, however, with the panicoid types since several common and widespread genera that produce panicoid phytoliths have the C_3 pathway. These genera include: Danthonia, Dichanthelium, Stipa and some Panicum species. It would be very convenient to use this system as a basis for determining the relative importance of C_3 and C_4 species in a grassland community but caution must be taken when the panicoid types are involved.

Palmer(1976) reported on the potential of using deposits of preserved grass cuticle as a paleoecological tool. She noted that the use of opal phytoliths alone presents certain limitations in that the only feature that can be determined with dispersed silica bodies is shape. Since some shapes are common to rather widely separated groups, these types may not provide much information with regard to taxonomic affinity of the grasses involved. Palmer notes that if cuticular remains are studied, additional information such as the distribution and occurrence of silica bodies, shape of subsidiary cells and the nature of the long cells and macrohairs can be obtained. With this additional information many more features are available to aid in assignment of the plant to subfamily, tribe or even genus. Comparisons of fossil material to prepared reference material from all the major grass species greatly aided identification.

In a study that evaluated qualitative differences between phytolith types as well as quantitative differences in opal phytolith content of soils, Kalisz and Stone (1984) investigated the history of the longleaf pine islands of the Ocala National Forest in Florida. In that study the authors determined the characteristic opal content of the soils of the pine islands, dumbbell phytoliths (panicoid) and diatom frustules, and the characteristic opal content of the soils of the surrounding scrubland (large ornamented spheroids) and then examined these deposits for evidence of vegetation changes. They found a pattern of decreasing opal content in the soils with distance away from the longleaf pine community islands in a manner that might suggest oscillation of the boundary between these communities. In discussing their results they mentioned a potential source of bias in the phytolith record. Small phytoliths, with proportionally greater surface area, are prone to more rapid dissolution than are larger, more stable forms. This can result in some phytolith types being underrepresented or absent from an assemblage this presents a problem with regard to the opal deposit accurately representing the plant community.

In an attempt to apply information derived from studies of opal phytolith deposits to a paleoecological problem in a manner similar to the stratigraphic use of fossil pollen and spore deposits, Carbone (1977) studied vegetation history associated with an archeological site in the Shenandoah Valley. A goal of the study was to compare conclusions from the phytolith data with the available pollen sequences that represent regional vegetation history to evaluate the usefulness of opal phytoliths as paleoecological indicators. Based on the opal phytolith content in the soil sequence that was examined, Carbone suggested that there was evidence for a transition from a forested environment during early Atlantic times to an environment with a much greater representation of grasses during the late Atlantic/early Subboreal times, and then back to forest in more recent times (Subatlantic to present). He noted that this shift would agree with vegetation changes associated with the Hypsithermal interval and with the occurrence of relict faunal populations. This sequence does not agree with the results of the study of regional pollen for the Shenandoah Valley but it does conform to the regional history for the Dismal Swamp of southeastern Virginia. Carbone is therefore inconclusive with interpretations of these results.

Yeck and Gray (1972), in a different approach to relating ecological implications to opal phytolith deposits, examined the relationship between phytolith size and annual precipitation. They isolated opal phytoliths from a number of soil types along an east-west transect in Oklahoma and then calculated the proportion of phytoliths of several size classes in each of these soils. The soils were selected from areas with different annual precipitation totals. They found that the eastern-most soil type (greatest annual precipitation) contained a greater proportion of larger phytoliths and that the western-most soil type (least annual precipitation) contained a greater proportion of the small size-class phytoliths, though no statistical analysis of this relationship was presented. The intermediate soil types did not conform to this relationship. Though the idea of evaluating the relationship between size and precipitation is a valid one, there are several problems with this analysis that confound interpretation along these lines. A strong vegetational gradient is present between their eastern and western sites. The eastern sites are dominated by panicoid grasses (*Andropogon*, *Sorghastrum* and *Schizachyrium*) and the western sites by eragrostoid grasses (*Buchloe*). Addressing the question in this manner major systematic or evolutionary differences between taxa were ignored in their study. The observed differences in phytolith size cannot be reliably attributed to precipitation differences. A more reliable means of approaching this relationship would be to study the size of phytoliths within a given species along a precipitation gradient to eliminate the effects of systematic differences.

Summary.

In this review of the opal phytolith literature pertaining to paleoecological applications, several conclusions can be drawn regarding the utility of these deposits. It is clear that quantitative data can, at best, give only very general information regarding broad vegetational changes. For instance, the determination of relative importance of grassland versus forest vegetation types has been well documented in this way. When "type-sets" or "morphological suites" are established for individual species, statistical analysis may indicate one species over another. Morphological differences in phytolith shape within the Poaceae may make possible determination of change in species dominance within the grassland community. These studies should be most successful when a survey is made of the opal content of all species that are potential contributors to the phytolith record.

There are several areas of investigation that need further attention so that opal phytoliths may be of greater utility in paleoecological studies. Differential production and weathering rates, which can result in quite biased microfossil records, have been recognized to be very important factors in palynological studies and have received considerable attention. These factors have not been addressed in studies of opal phytolith deposits. It was mentioned above that there is some evidence for differential dissolution rates with the smaller opal particles being destroyed at a faster rate. Differential production rates have not been addressed at all and are of equal importance. Some information regarding these topics will be presented.

Opal phytolith evidence of vegetation history of the Maxton Plains.

Methods.

The procedures involved in the various aspects of the opal phytolith study will be outlined here. This will include soil sample collection and phytolith isolation, reference sample preparation, phytolith counts and ternary diagram preparation.

Sample preparation

Soil samples for study of opal phytoliths were collected from a variety of localities. Portions of the soil samples that were collected in July 1983 for analysis of pH, moisture, organics and texture were reserved for phytolith studies. As was mentioned in an earlier section, these soil samples represent the entire soil profile to the top of the shallow mineral zone that overlies the bedrock. Soil samples for all alvar sites except 29-2 are composite samples, composed of six samples distributed throughout the alvar site.

Soil samples were also collected in June 1984 from a number of other alvar sites. These sites were all lacking the usual dominant species, *Sporobolus heterolepis*, though a few of them supported very small populations of *Schizachyrium scoparium* which were usually restricted to isolated localities in the transition zones. Soil samples were collected from these sites in an attempt to determine to what extent these species may have lived at these sites in the past. These soil samples were collected in a manner similar to that described above.

In addition to collecting soils representitive of both, alvar sites dominated by Sporobolus and Schizachyrium, and alvar sites lacking these dominants, soils have been collected from along four transects that extend from a Sporobolus-Schizachyrium dominated alvar, through an upland transition and into the forest. These transects were located in several different kinds of transitions in an attempt to record different patterns of vegetation change. The transects were established in such a way that they each started in the alvar in an area not influenced by the transition. The transects were of various lengths but all ended well into the forest. Soils were collected at regular intervals along the transects. At each sample point several soil samples from the immediate vicinity were collected and combined. Composite soil samples were taken here, and in the other localities, with the reasoning that microtopographic variation may in some way influence the opal phytolith deposition or preservation characteristics and thus could be a serious problem in single point samples. Positions of the transects are shown on the map of the Maxton Plains in Appendix A.

Preparation of soil samples

Procedures followed in isolating the opal phytolith component of the soil samples:

1) Dry soil samples ($100^{o}C$ overnight, forced air drying oven) to facilitate dry sieving.

2) Homogenize sample thoroughly and sieve through 2mm screen to remove gravel and large pieces of organic litter.

3) Divide samples into two equal parts. One sample reserved for future use if needed.

4) Sieve one sample again through a 425 micron screen. This upper limit for particle size was selected to remove the greatest amount of fine organic litter that could be eliminated from the sample yet allow as much of the large opaline material as possible to be retained in the sample. No minimum size limit was imposed.

5) Homogenize sample and remove 10 ml subsample for processing.

6) Place sample in a 90 ml plastic test tube or a 250 ml beaker and add a small amount (ca 10 ml) of 10% HCl. Since for samples which contain large amounts of carbonates it is necessary to be very careful when adding HCl. After the reaction slowed add another 10 ml of HCl. This procedure was continued, stirring frequently, until the rate of reaction slowed considerably.

7) Add 10% HCl to at least three times the volume of the sample and let stand overnight.

8) Centrifuge samples at moderate speed for 20 minutes. Remove supernatant liquid by aspirator.

9) Wash residue three times with distilled water. In each wash add water to 2/3 capacity of tubes, then stir thoroughly, centrifug, and remove liquid.

10) To oxidize organic components, transfer sample to glass tubes and add ca 20 ml of Schulze solution (5:1 conc. HNO_3: 10% $KClO_3$ soln.). Stir with a glass rod. If the reaction is strong, add equal volume of water and place the tube in ice. Organic-rich soils are particularly reactive.

11) Add Schulze soln. in small quantities; stir frequently, until it is certain that the samples will not flow over the top of the tubes. Some samples required 250 ml beakers.

12) After the reaction rate is reduced greatly, add Schulze soln. to 1/2 capacity of the tubes and let stand overnight.

13) Centrifuge samples and remove liquid.

14) Add fresh Schulze soln. and place samples on steam table for several hours until all reaction had ended.

15) Wash samples three times with distilled water.

16) Add 5% KOH soln. (2 times volume of the sample) and let stand for ca. 10 minutes. Do not be put in a steam table since KOH will dissolve opaline silica when hot.

17) Wash samples until supernatant liquid is clear. For some highly organic samples this often requires as many as 10 washes.

18) After all humic acids are removed by washing, dehydrate with 90% alcohol followed by acetone.

19) Transfer samples to small tapered 15 ml centrifuge tubes with acetone.

20) Heavy liquid separation is utilized to remove the heavy minerals from the opal component of the sample. Add bromoform, 2.3, adjusted with acetone, to the sample such

that the liquid level was ca 1 cm above the sediment.

21) After stirring, centrifuge sample at moderate speed for 10 minutes.

22) Remove the supernatant liquid, with floating opal, by pipette to a separate tube.

23) Repeat procedure three times to remove all opal from the sample.

24) Remove bromoform from the sample by diluting with enough acetone to sink the opal (i.e., reduce density of the liquid to less than 2.0 sp. gr.) and then centrifuging for 15 minutes. Save liquid for bromoform reclamation.

25) Wash samples with alcohol three times; transfer to distilled water and store in small vials.

Collection and preparation of reference materials

Reference material from as many opal producing taxa as possible was prepared so that dispersed opal in the soils could be recognized whenever possible. For this analysis portions of leaves, stems and reproductive structures were selected from several specimens of each species, collected at maturity, so that phytolith morphology variability within and between individuals could be accounted for in the reference sample. The following is the procedure followed in preparing reference materials. Species examined for opal phytolith content are marked with an asterisk in Appendix C.

Preparation procedures for reference samples

1) Select a number of leaves and stems from several mature individuals.

2) Wash thoroughly with water then rinse with distilled

water.

3) Break ortear plant material into pieces that can be placed in glass centrifuge tubes.

4) Fill tubes to 1/2 capasity with Schulze soln.

5) Place tubes in steam table for several hours until all plant material is digested. Stirr or agitate occasionally.

6) Centrifuge at moderate speed for 15 minutes and remove liquid with aspirator.

7) Wash three times with distilled water.

8) If samples are clean transfer to vials, otherwise repeat treatment with Schulze soln.

Preparation of slides for study

Slides for both reference samples and soil samples were prepared in the same manner. Since opal has a refractive index very near to that of glass, it is important to use a mountant that has a high index of refractance (RI) to provide as much contrast with the opal as possible. A mountant that I found to be quite useful because of the high RI was Naphrax, available through Northern Biological Supply, England. For a comparison of the utility of several mountants in observing siliceous materials see Wee (1983). The following is a standard procedure for preparation of slides from reference samples and soil samples.

1) Agitate vials thoroughly to disperse sample.

2) For reference samples, remove approximately 2 ml of sample by pipette and spread evenly across a coverslip on a slide warming table (set at 40°C). For soil samples, remove

the same volume of sample but place in beaker and dilute with approximately 10 ml of distilled water. Mix this thoroughly and then transfer enough to cover the surface of the coverslip. Some soil sample opal residues are very concentrated and must be diluted even further so that the slides will be useful.

3) Let residue on coverslip dry completely on warming table.

4) Place two drops of Naphrax on coverslip and then carefully lower slide to contact the coverslip.

5) The slide can be left upright to dry on a heated slide table (60°C.) for several days or the solvent can be boiled off rapidly on a hot plate.

Identifying characteristic morphologies of opal phytoliths in reference samples

Slides were made of all reference samples and studied for characteristic and repetitive morphologies. Unusual, rare morphologies were diagrammed when observed but were generally not used. Rare forms are not likely to be encountered often in soil samples and so will be of little use. Phytoliths with unique repetitive morphologies are the most useful paleoecologically. Diagrams and photographs were made for comparison between species.

Counting of opal phytoliths in soil samples

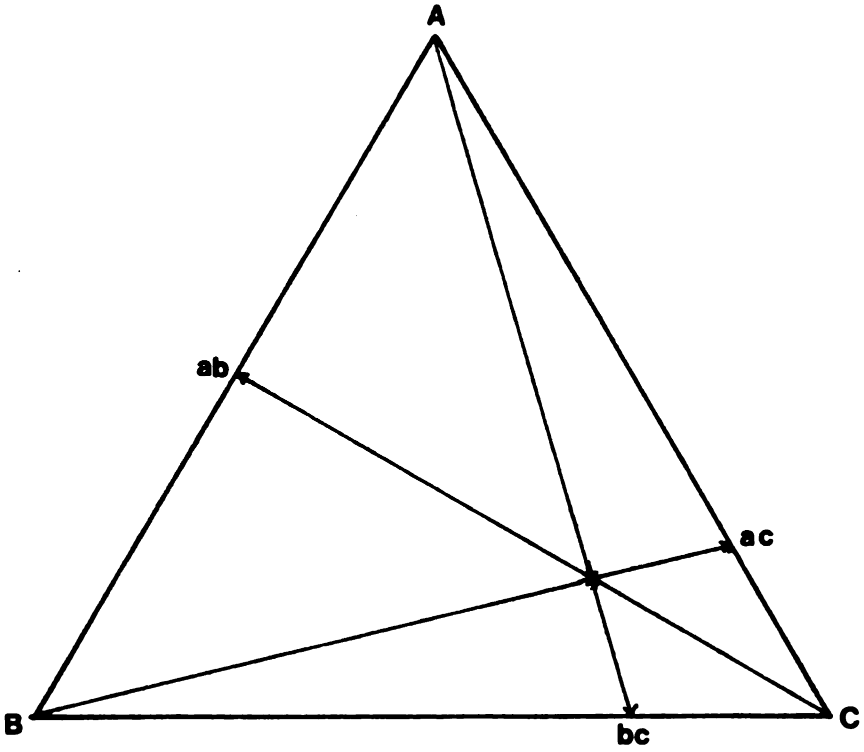
The quantity of opal material in most slides was quite high. Each slide was first scanned to check for any irregularities in distribution of opal material on the slide. Several randomly located traverses were then made across the slide in which all phytoliths were counted. The following morphological categories of phytoliths were recognized: pooid, panicoid, chloridoid, long cell and unidentified. Diatoms were aslo noted. The unidentified opal phytoliths appear to have been produced by grasses but could not be assigned to one of the first three categories. In most slides 250 phytoliths were counted. In the samples that had a minimal opal content 100 phytoliths were counted.

In addition to counting phytoliths, each slide was rated for its content of fine particulate opal and the remains of woody material. The fine opal component was ranked from 1 (minimal) to 6 (maximum) while the woody material was ranked 1 to 4. The determination of these components was done separately after the phytolith counts were finished. All slides were analyzed and grouped according to content.

Use of ternary diagrams in representing opal phytolith data

Relationships between selected phytolith morphologies were examined by plotting the phytolith data on ternary diagrams. An advantage of using this diagram is that it can use both percentage data and absolute frequency data and give the same plotted point on the diagram.

Figure 8 shows a ternary diagram with the relationship between three morphological types, categories A, B and C. In this case percent data is being used and is presented below the diagram. Note that category D is not being considered in this diagram. The position of the point on the diagram is determined by the proportional relationships



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Category	Percent
A	20
B	20
C	40
D	20

Figure 8 Ternary diagram representing the relationship between categories A, B and C. This figure demonstrates the procedures involved in plotting either percentage data or count data.

in pairwise comparisons of categories. Categories A and B are both represented by 20%, thus there is a 50:50 relationship between these groups. This relationship would be plotted as a point ("ab") midway between A and B on the left leg of the triangle. A line is then drawn, originating at the opposite corner C, and extending to point "ab". Similarly, the relationship between A and C is determined to be 1:2 and a point ("ac") is then plotted on the right leg of the triangle two thirds the distance from A to C. A line is then drawn from the opposite corner B to point "ac". The intersection of these lines is the point that represents the relationship between these three categories. Plotting the third line is not necessary since it should intersect the other two at the same point but doing so is a good check against errors. Many samples can be plotted on the same diagram, either to represent the variation in the relationship between samples or to represent a trend in the relationship as it might change along a transect or stratigraphic sequence.

Plotting of these relationships, a very laborious process when done manually, was greatly aided by a program written in BASIC by Dr. Ralph E. Taggart. Through use of this program many different combinations of phytolith categories could be tried to find those that most clearly showed meaningful patterns. A feature of this program that is quite useful is a routine that will calculate a measure of dispersion of the sample points on the diagram. The resulting ellipse can be thought of as a pseudo-variance.

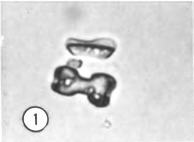
"Pseudo" because it is not a true statistical measure. It is a measure of the dispersion of the X-Y coordinates of the sample points as they are calculated by the program. Through the use of this measure, differences between populations, in this case opal content of soils from alvar sites dominated by *Sporobolus heterolepis* and *Schizachyrium scoparium* may be compared with alvar sites lacking dominance by these species.

Results and discussion.

Distinction between phytolith morphologies

Study of the opal material isolated in the reference samplesmade possible the recognitionof the major phytolith morphologies in the soil deposits. Figures 9-11 present photographs of the common phytolith types in the reference samples. From these photographs it can be seen that the pooid species, *Agropyron trachycaulum*, *Bromus kalmii*, *Festuca ovina*, *Deschampsia cespitosa*, *Phleum pratense*, *Poa compressa* and *Poa pratensis*, are discinctive as a group. *Schizachyrium scoparium*, *Dichanthelium accuminatum* and *Danthonia spicata* have panicoid-type phytoliths. *S. scoparium* has a dumbbell phytolith morphology with a long shank and round ends that can be distinguished from the common dumbbell-shaped form found in *D. spicata*, which has a shorter shank and squared ends. However, the many intermediate types in both species cannot be distinguished. It seemed pointless to identify some panicoid phytoliths to

Figure 9. Opal phytoliths isolated from reference materials. *Danthonia spicata* (1-7), *Schizachyrium scoparium* (8-11). For all figures, scale bar = 20μm.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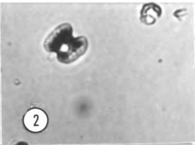
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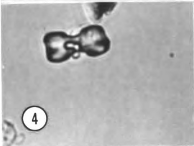
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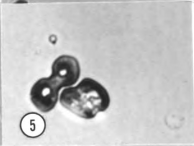
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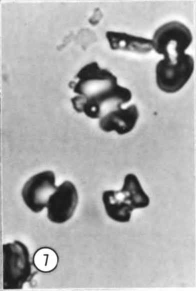
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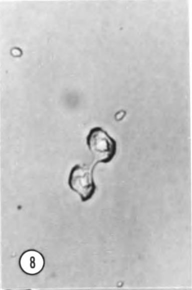
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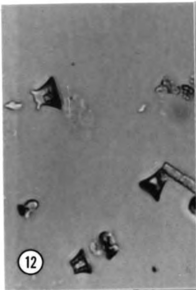
Figure 10. Opal phytoliths isolated from reference materials. *Sporobolus heterolepis* (12-16), *Bromus kalmii* (17-18). For all figures, scale bar = 20µm.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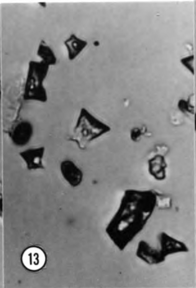
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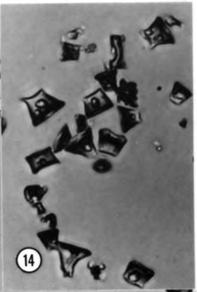
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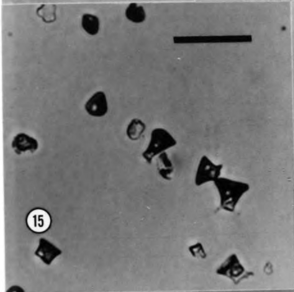
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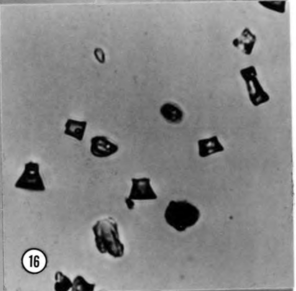
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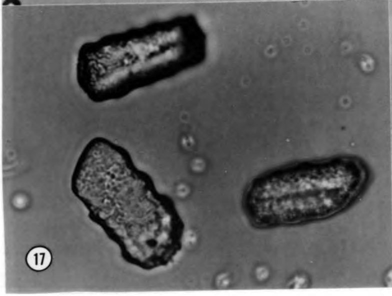
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Figure 11. Opal phytoliths isolated from reference materials. *Poa pratense* (19-23), *Agropyron trachycaulum* (24-26), *Festuca ovina* (27-31). For all figures, scale bar = 20μm.


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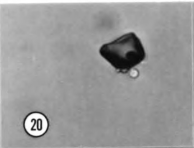
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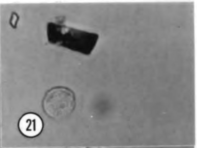
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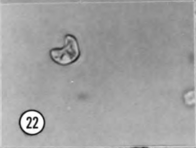
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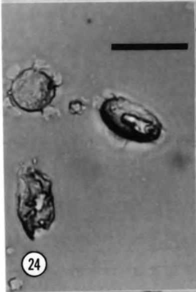
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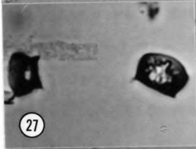
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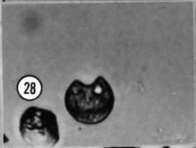
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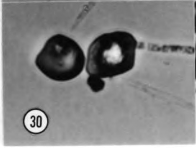
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species when many other panicoids could not be so assigned. It would be helpful to be able to recognize consistently the phytoliths of these two species since they overlap somewhat in the kinds of areas that they occupy on the alvars. Sporobolus heterolepis and S. vaginiflorus are the only species producing chloridoid-type phytoliths, of which S. heterolepis is by far the most important with regard to volume of opal production because of its strong dominance on the alvars. Phytoliths of the two Sporobolus species are not distinguishable in reference samples.

Very few distinctive morphologic forms of opal were found in species other than grasses. Carex species yielded only nondescript plates and fragments and some silicified long cells. No cone-like phytoliths were found as reported by Mehra and Sharma (1965). Many other species also produced plate-like structures, fine rods, portions of epidermis with silicified intercellular spaces, globules and fragments with few distinctive types noted. Of those species that appeared to produce a distinctive phytolith morphology, none was present in numbers great enough to be useful as an indicator in the soil. A diagnostic but rare phytolith will be of no utility paleoecologically.

Vegetation history as examined through opal phytolith deposits in the soils

Notes on the vegetation along the transects and from the sites lacking the dominance of S. heterolepis and S.scoparium are summarized below.

Transects:

28/33-1 transect #1- This transect extends from an alvar into an old growth of aspen. The transect extends roughly north-south through a relatively narrow transition zone. *Sporobolus* is present to third sample point; *Schizachyrium* is present to sixth sample point; *Danthonia* is present in nearly all samples. The aspen canopy is developed at the fourth sample point and is present in samples 5 and 6.

28/33-1 transect #2- This transect starts at the same location as transect #1 but was extended east into a conifer forest dominated by *Thuja occidentalis* and *Picea glauca* through a rather abrupt transition zone. *Sporobolus* is present in the first and second samples, *Schizachyrium* and *Danthonia* are present in the first to third samples; only *Carex eburnea* is present under the dense canopy of conifers at the fourth sample point.

34-1 east transect- This is located in the east side of site 34-1. The transect extends north into a conifer forest through an east-west transition. *Sporobolus* is present in the first and second sample points, *Schizachyrium* and *Danthonia* are present in the first to third samples, only *Carex* and pooid grass species are present under the well develped canopy at the fourth sample site

34-1 north transect- Located in the north end of site 34-1, this transect extends west into an aspen and conifer forest. The transition zone is rather narrow and extends north-south. *Sporobolus* is not nearby after the second sample while *Schizachyrium* is nearby in all but sample 3, *Danthonia* is nearby for only the first two samples.

West road transect- This transect is located in the area between sites 28/33-1 and 34-5 that is supporting many young aspen. The transition has a broad zone of young aspen which gives way to a mature conifer forest with *Picea* and *Thuja*. *Sporobolus* is present to the third sample, *Danthonia* is present only at the third sample and *Schizachyium* is not present near any of the sample localities.

Sites lacking dominance by *Sporobolus* and *Schizachyrium*:

Site 36-2, one bunch of *Sporobolus heterolepis* was found in this site. *Schizachyrium scoparium* was also found near one edge of the site.

Site 36-4, both of these species were found in restricted areas along the southern transition of the site.

Site 36-7, *S. scoparium* was found in a restricted portion of the transition.

Site 36-5, *S. scoparium* was found near the edge of the site.

Site 36-6, *S. scoparium* is present near one edge and a dead *Picea* tree is in the center.

The sites that were found to support small populations of *S. heterolepis* and/or *S. scoparium* are very curious. It is questioned whether these species were once more abundant in these sites or whether they have always been so restricted. It is possible that these species have been eliminated by grazing from all but the most sheltered areas of these sites. One of the sites that is unusual in this regard is site 36-2. As far as can be determined, this site supports only one bunch or clone of *Sporobolus heterolepis* which is located in the central part of the alvar, not associated with an alvar margin.

The results of the opal phytolith counts are presented in Table 10. The phytolith contents of the soils from the five transects, the alvar sites dominated by *Sporobolus heterolepis* and *Schizachyrium scoparium* and the sites lacking dominance by these species, as well as several samples from site 33-2 are presented in this table. The opal content of the soils from the *Sporobolus* and *Schizachyrium* dominated alvars is quite different from that of the alvars lacking these dominants. Soils were examined from nine sites lacking these dominants. Samples representitive of the *Sporobolus* and *Schizachyrium* dominated alvars are based on soils from a number of alvar sites plus the first sample from each of the transects. The first sample from West Road Transect was not used here since there was some doubt as to the degree of disturbance of this area.

It is interesting to note that only one of the sites lacking *Sporobolus* and *Schizachyrium* had opal deposits that contained any chloridoid phytoliths. This site is located between sites 33-2 and 33-4 in an area that was observed to have been open when the 1939 aerial photographs were taken.

A statistical analysis of the differences in phytolith composition between these two groups of sites shows several significant differences. Table 11 presents the results of

Table 10. Number of opal phytoliths observed in soil samples from both the alvar sites dominated by Sporobolus and Schizachyrium and the alvar sites lacking dominance by these species, and the transects indicated.

								RANK	
SITE	POOID	PANI COID	CHLOR IDOID	LONG CELLS	DIA- TOMS	UNI- DENT.	TOTAL	FINE OPAL	WOODY FRAGMTS
34-1N 0m.	30	54	42	58	4	12	200	4	2
34-1N 20m.	35	61	21	51	22	10	200	5	3
34-1N 40m.	45	50	3	145	0	7	250	3	2
34-1N 60m.	39	47	4	136	1	23	250	2	2
34-1N 80m.	25	72	25	114	0	14	250	4	2
34-1E 0m.	49	73	16	89	15	8	250	4	1
34-1E 20m.	--	--	--	--	--	--	--	-	-
34-1E 40m.	36	94	15	93	1	11	250	4	2
34-1E 60m.	20	116	5	99	1	9	250	3	2
34-1E 80m.	33	89	18	96	1	13	250	3	2
34-1E100m.	15	107	20	100	1	7	250	4	2
WRC 1	25	21	3	170	17	14	250	1	3
WRC 2	26	51	13	124	31	5	250	2	3
WRC 3	37	43	13	136	13	8	250	2	3
WRC 4	40	77	11	102	11	9	250	4	2
Trns1 0m.	20	81	21	109	4	15	250	3	2
Trns1 10m.	46	31	42	122	2	7	250	3	4
Trns1 20m.	17	119	17	93	1	3	250	3	2
Trns1 30m.	21	61	8	150	1	9	250	3	4
Trns1 40m.	27	97	4	116	3	3	250	4	3
Trns1 50m.	20	91	2	131	1	5	250	3	2
Trns1 60m.	23	68	4	148	0	7	250	3	3
Trns2 0m.	20	81	21	109	4	15	250	3	2
Trns2 10m.	26	72	11	130	3	8	250	3	2
Trns2 20m.	41	100	13	85	2	9	250	3	3
Trns2 30m.	22	104	6	107	2	9	250	3	3

Table 10. (continued)

Alvar sites lacking dominance by *Sporobolus* and *Schizachyrium*

SITE	POOID	PANI COID	CHLOR IDOID	LONG CELLS	DIA- TOMS	UNI- DENT.	TOTAL	FINE OPAL	WOODY FRAGMTS
34-3	18	41	0	33	1	7	100	5	1
34-2	14	16	0	62	2	6	100	4	3
33-6	13	17	0	67	0	3	100	2	3
btwn33 3-4	21	18	2	50	4	5	100	5	1
35-2	16	4	0	75	1	4	100	2	2
36-2	26	1	0	70	0	3	100	1	2
36-4	28	2	0	64	3	3	100	3	2
36-7	13	2	0	75	7	3	100	1	2
36-5	17	0	0	74	6	3	100	2	3
36-6	--	--	--	--	--	--	--	2	1
Alvar sites dominated by *Sporobolus* and *Schizachyrium*									
28/29-1	37	47	23	130	7	6	250	2	3
29-2 T2-#2	37	46	14	146	2	5	250	3	2
29-2 T5-#4	26	37	10	167	4	6	250	3	1
33-2	53	30	12	131	14	10	250	5	2
wet edge	17	19	1	30	174	9	250	6	1
sw corner	47	3	0	47	36	17	150	2	2
center	33	16	29	131	14	27	250	1	3
conifer isl	50	8	0	136	0	6	200	2	2
old aspen	32	55	10	91	4	8	200	3	4
ne end	57	24	7	99	0	13	200	3	3

Table 11. Differences in composition of opal phytolith deposits in soils from alvar sites dominated by *Sporobolus* and *Schizachyrium* (Sh/Ss) and alvars lacking the dominance of these species (Others).

Phytolith	Mean Sh/Ss	Mean Other	T	Prob.(df=15)
Chloridoid	16.78	0.90	8.21*	3.110E-7
Panicoid	25.82	16.26	1.90*	.0386
Long Cells	44.87	52.91	-2.26*	.0194
Pooid	22.28	25.24	-1.59	.0665
Diatoms	10.33	7.85	1.09	.1456
Unidentified	11.70	11.54	0.11	.4571

Percentage data are arcsine transformed.

this statistical analysis in which arcsine transformed percent data are used. It can be seen that there are significant differences between these sites in the content of chloridoid, panicoid and long cell phytoliths. Opal deposits from the *Sporobolus* and *Schizachyrium* dominated sites contained a much greater quantity of grass opal than did the deposits from the other sites.

These differences in total grass opal content and the distribution among the morphology classes can be interpreted in several ways. One interpretation is that these groups of sites have not supported similar vegetation types in the past. A second interpretation is that the degradation rate of opal in these soils is rapid enough that, as vegetation changes, the phytolith assemblage in the soil changes accordingly. The opal phytolith deposits would thus be primarily representitive of the present vegetation, with little evidence of the former vegetation type remaining. Evidence for both of these interpretations will be presented. In support of the former interpretation is the fact that chloridoid phytoliths, presumably from *Sporobolus heterolepis*, have been recorded in soils from transect samples in the forest where no *Sporbolus* now occurs. These phytoliths must have remained in the soils for a significant amount of time since the transects end in well developed forest. Further evidence for this conclusion is the fact that the soils from sites dominated by *Sporobolus* and *Schizachyrium* tend to have a greater number of panicoid phytoliths than pooid phytoliths, whereas the reverse condition is true of the soils from sites lacking dominance by these species. Finally the difference in quantity of grass opal between these two groups of sites is evidence in support of this conclusion.

Evidence that could be taken to implicate the latter mentioned interpretation is the fact that even when Sporobolus heterolepis is the dominant grass species in a site, it is represented in the opal phytolith assemblage by only 11 to 39 percent of the silica cell phytoliths (pooid, panicoid, chloridoid). This underrepresentation is due, at least in part, to the differences in epidermal structure (i.e., numberand arrangement of silica cells) between the subfamilies. The biased representation could also be partly due to differential weathering rates between the morphology classes. If the small chloridoid phytoliths weather at a faster rate than the much larger panicoid and long cell types, then it is possible that opal phytolith evidence of a Sporobolus-dominated alvar could be relatively short lived. Differential weathering does not, however, explain the differences in total grass opal that exist between these groups of sites.

There are several mechanisms by which opal phytoliths can be transported from one area to another, thereby introducing a source of error into the analysis. Some of these mechanisms could also be important in the above mentioned representation bias between panicoid and chloridoid forms. Phytoliths can be transported in dusts, through sheet flow of water across the soil surface and by herbivorous animals. Sheet flow should not be a problem in this investigation since the upland transitions are being studied. Scats from deer and rabbit, two major browsing vertebrate species, and the gut contents from several grasshoppers (*Melanoplus* sp.) were examined for opal phytolith content. The scats were collected in June 1984 from several alvar sites (27-24 deer, 33-2 rabbit, 5/6-2 rabbit) and appeared to be relatively fresh. The grasshoppers were collected in September 1984 from site 28/29-1.

The opal content of the fecal material of both the deer and rabbit consisted of large quantities of fine particulate material, frequent diatoms and long cell phytoliths and a smaller number of pooid phytoliths. No chloridoid or panicoid phytoliths were observed. It is possible that these animals will only browse on *Sporobolus* and *Schizachyrium* later in the season when the plants are producing seed. Since I examined fecal material produced before these grasses flowered I cannot say for sure that these animals do not appear to be important with regard to transport of panicoid and chloridoid phytoliths.

The grasshopper gut contents consisted of fine particulate opal, long cell and pooid phytoliths and some diatoms. Grasshoppers appear to avoid *Sporobolus* and *Schizachyrium* as a food source. Large pieces of epidermis from a pooid grass species were commonly found in this material. It is possible that grasshoppers could transport pooid phytoliths into adjacent areas.

The importance of transport of opal phytoliths by wind was not addressed here. The magnitude of this source of introduced opal is unknown but is assumed to be low for several reasons. The study area is far removed from any extensive areas of grassland vegetation or open agricultural land, features that can be sources of large quantities of wind-blown phytoliths. I would expect that the opal that is introduced in this manner would be deposited in a more or less even fashion. It is possible that the bias in representation toward panicoid phytoliths could be partly explained by a panicoid dominated aeolian deposit. I can do no more than speculate in this regard since I have not collected dust and rain samples necessary to assess this factor.

It is hoped that through examination of the opal phytolith content of the soils along the transects, some portion of the history of these grassland-forest boundaries can be understood. From Table 10 it can be seen that chloridoid phytoliths were encountered in all soil samples from the transects studied, though they usually declined somewhat in number with distance into the forest. It was noted that Sporobolus heterolepis did not occur in the vicinity of the last sample on any of the transects. The occurrence of chloridoid phytoliths and the general abundance of grass opal in the soils suggests some influence of grassland vegetation in these forested areas.

It was thought that remains of diatoms might also serve as an indication of open conditions since they appear to be components of a seasonal, perhaps spring and early summer, soil algal community. Remains of diatoms have been recorded both in sites dominated by Sporobolus and Schizachyrium and in sites lacking these dominants. It is reasoned that if diatoms cannot be supported in forested areas because of low light levels, then their occurrence in forest soils might be an indication of an earlier period of more open vegetation. The phytolith data from the transects show that in all cases the number of diatom frustules decreases with distance into the forest with two of the transects having no diatom remains encountered in the last sample.

Several factors should be kept in mind when considering the significance of the diatom remains. First, diatom remains may be prone to relatively rapid dissolution in upland soils, given their intricate ornamentation and greater surface area, and thus would be underrepresented or absent from some deposits. Second, depending on the composition and orientation of a transition, the potential to support diatom populations could be quite different. For example, the transect located at the north end of site 34-1 extends westward into a conifer-dominated forest. The canopy is well developed and since the forest extends to the west and to the south, the available light throughout the day is quite reduced. In contrast, 28/33-1 transect #2 extends to the east into a heavy conifer forest. The canopy in this area is heavier that in the previously mentioned area. However, due to a well developed browse line and open grassland to the south and west, there is more light penetrating into this forested region. Accordingly, it is not surprising that diatoms are recorded in the last sample from this transect. There are some drainage differences between these transects that could also be important in the occurrence of diatom remains.

A third transect that shows very different patterns with respect to diatom remains is the West Road Transect. In this instance the transition is dominated by aspen in all but the last station which has a canopy consisting primarily of conifers. This transect is in an area that is quite moist, at least during the early part of the growing season. An area that is dominated by aspen will not usually impose much light reduction until sometime in early June and thus may not present much of a limiting influence on diatom populations. It can be seen that though there is potential in the use of diatom remains as indicators of a period of open vegetation, differential weathering rates and characteristics of the individual transitions must be considered.

The rating of fine opal content and woody material content in the soil samples do not appear to show any consistent patterns. The sample with the highest fine particulate content was from the wet edge (south) of site 33-2. Some other relatively moist samples, such as 34-1 north-20 meters, also had abundant quantities of fine opal while still others, such as the first three samples of the west road transect, had relatively little fine opal material. Some relatively well drained sites had high ratings of fine opal content. Similarly, the content of woody material appeared to vary without pattern.

Though some patterns in the phytolith data can be recognized in Table 10, many other relationships may be obscured in this tabular summary. It is hoped that through the use of the ternary diagrams some of these less obvious patterns and relationships will be made more apparent. The diagrams are being used to help in evaluating the two primary questions being asked in this investigation of the vegetation history: 1) is there any evidence of Sporobolus heterolepis and Schizachyrium scoparium dominance in the alvars thatpresently lack these species; 2) is there any evidence of significant grassland influence in the transitions and forested areas adjacent to the alvars.

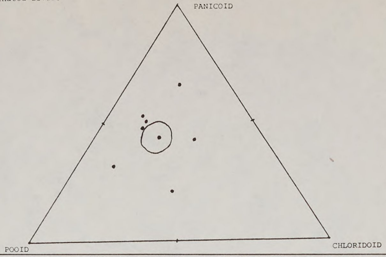
In using the ternary diagrams to examine the phytolith data from the transects, it was reasoned that the morphology classes showing significant differences between the two groups of alvar sites should be most useful as indicators of any vegetation changes. These groups are the panicoid, chloridoid and long cell phytoliths. In the following diagrams several examples of different combinations of phytolith morphologies will be presented. In each of these figures the top two ternary diagrams represent the differences in the phytolith assemblages between the alvar sites dominated by Sporobolus heterolepis and Schizachyrium scoparium and the alvars lacking dominance by these species. The circles on these diagrams represent a pseudovariance or a measure of the dispersion of the sample points on the diagram. The lower four ternary diagrams represent the phytolith assemblages in the transects indicated. Arrows indicate the sequence of samples along the transect. It is suggested that 28/33-1 transect #1 and 34-1 east transect will share more common characteristics in their opal assemblages because they are located in comparable transitions with similar physical features.

Figure 12 represents the relationships between the pooid, panicoid and chloridoid phytoliths. In this figure it can be seen that the phytolith assemblages representing the two groups of alvar sites are quite different. In addition, each of these transects shows unique patternsof change in its opal phytolith assemblages. The above mentioned transects (28/29-1 trans. #1 and 34-1 east) appear to be similar in that they both show a trend toward increasing dominance by panicoid types, 34-1 east more clearly than 28/33-1 trans. #1. The other two transects do not show any distinctive trends. It is interesting to note that nearly all of the plotted points for the transects fall within the scatter of points that represents the alvar sites dominated by Sporobolus and Schizachyrium.

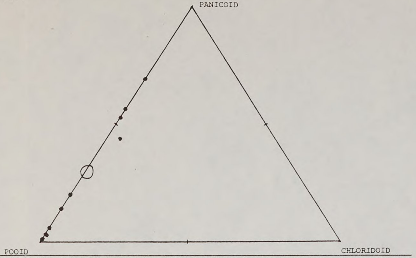
Figure 13 presents the relationships between diatom, panicoid and chloridoid phytoliths in these same sites and transects. From this set of diagrams several significant

Figure 12 Ternary diagrams representing the relationships between pooid, panicoid and chloridoid opal phytoliths.

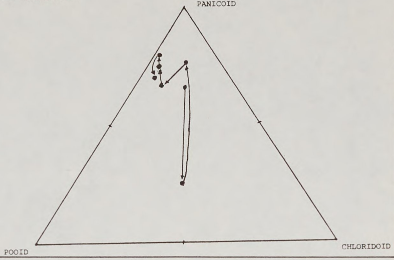
Sporobolus and *Schizachyrium* dominated alvars



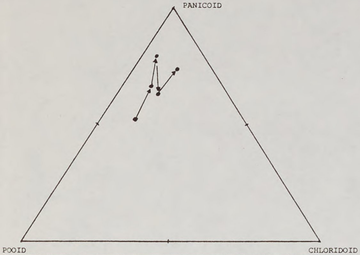
Alvars lacking these dominants



28/33-1 Transect #1



34-1 East Transect



West Road Camp Transect

34-1 North Transect

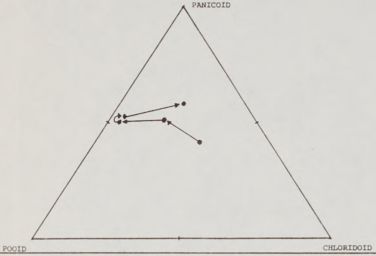
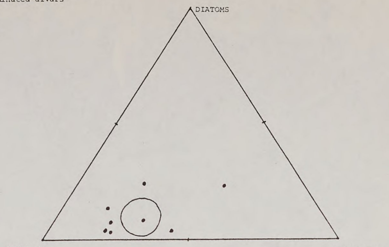
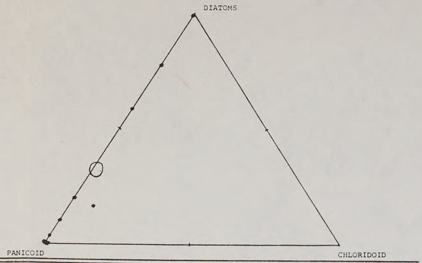


Figure 13 Ternary diagrams representing the relationships between panicoid and chloridoid phytoliths and diatom remains.

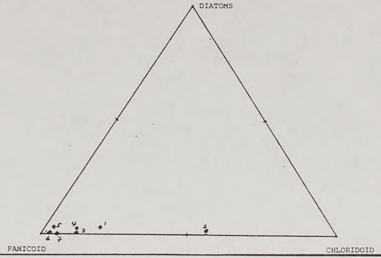
Sporobolus and Schizachyrium dominated alvars



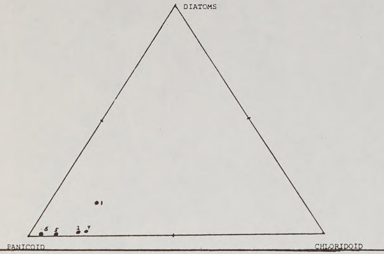
Alvars lacking these dominants



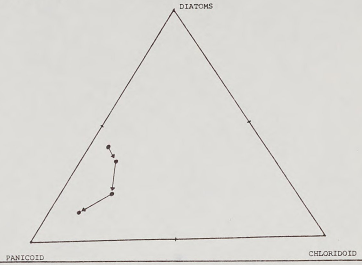
28/33-1 Transect #1



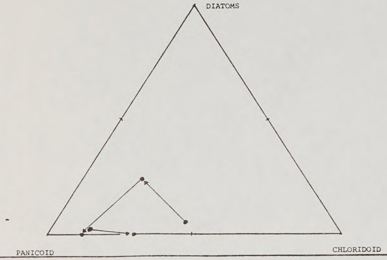
34-1 East Transect



West Road Camp Transect



34-1 North Transect



features can be seen. This combination of phytolith morphologies also allows a clear distinction between the two groups of sites, represented in the top two ternary diagrams. It can be seen that this difference is primarily due to the presence of the chloridoid phytoliths in the *Sporobolus* and *Schizachyrium* dominated sites. There appears to be much more variability in the proportional relationship between panicoids and diatoms in the sites lacking *Sporobolus* and *Schizachyrium* dominance. This could be a result of variability in moisture conditions between these sites.

The first two transects again appear to be more similar toeach other in that the plotted points for both transects are rather tightly clustered and variable in the panicoid corner of the diagrams. These points show, for the most part, a stronger dominance by panicoid phytoliths than is seen in the alvars dominated by *Sporobolus* and *Schizachyrium*. This is not the case with the lower two transects represented on this figure. This could be interpreted to suggest that *Schizachyrium scoparium* and/or *Danthonia spicata* have been more important in 28/33-1 transect #1 and 34-1 east transect than has *Sporobolus heterolepis*. This could be an indication that these transitions are relatively more stable.

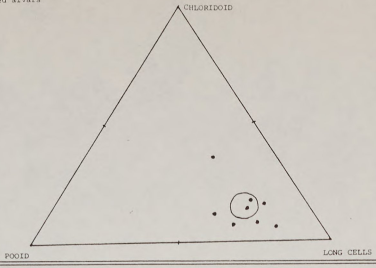
The diagram for the west road transect illustrates quite well the relationships with the diatom remains. This ternary diagram shows that the proportional relationships between panicoids and diatoms in this transect is quite similar to that of the open alvars. This is likely due to the deciduous cover of the aspen dominated transition.

Figure 14 illustrates the proportional relationships between pooid, chloridoid and long cell phytoliths in the same sites and transects as discussed above. In this figure it can be seen that the ternary diagrams representing the two groups of alvar sites are different only with regard to the chloridoid content. The proportional relationships between pooids and long cells appear to be nearly identical between these groups. There appears to be little that distinguishes the first two transects from the others using this combination of morphologies. All but the west road transect show an increasing dominance of long cells over pooids with distance into the forest. Each of these transects, however, shows unique patterns with respect to relationships with the chloridoid phytoliths. Though each of these transects shows trends of one sort or another, it is difficult to make any conclusions as to their significance. This may be primarily due to the minimal differences that exist between the ternary diagrams representing the two groups of alvar sites.

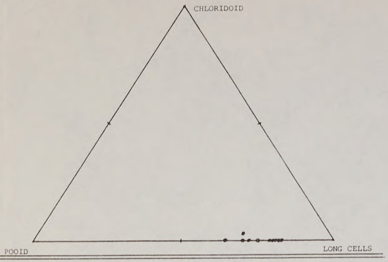
Finally, figure 15 presents the relationships between the three silica cell types (pooid, panicoid, chloridoid), long cells and diatoms. In this figure it can be seen that there is little discernible difference between the ternary diagrams of the two groups of alvar sites. There is a quite tight cluster of points in the diagram representing the 34-1

Figure 14 Ternary diagrams representing the relationships between pooid, chloridoid and long cell phytoliths.

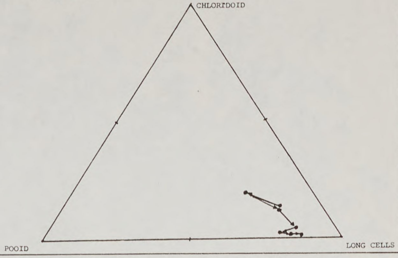
Sporobolus and *Schizachyrium*
dominated alvars



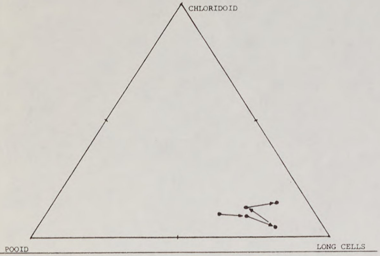
Alvars lacking these
dominants



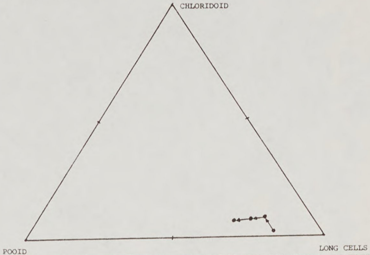
28/33-1 Transect #1



34-1 East Transect



West Road Camp Transect



34-1 North Transect

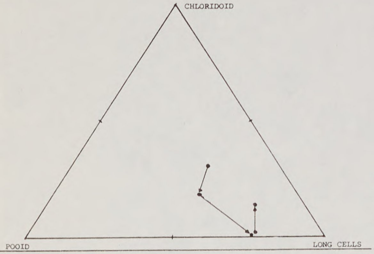


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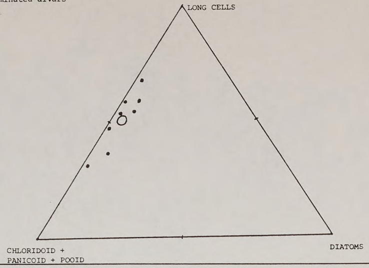
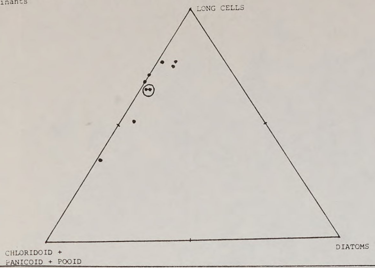
Figure 15 Ternary diagrams representing the relationships between silica cell and long cell phytoliths and diatom remains.

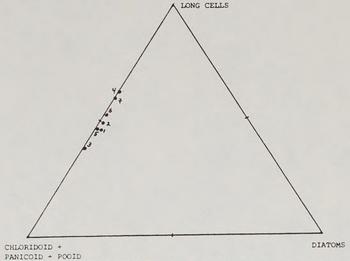
Sporobolus and *Schizachyrium* dominated alvars



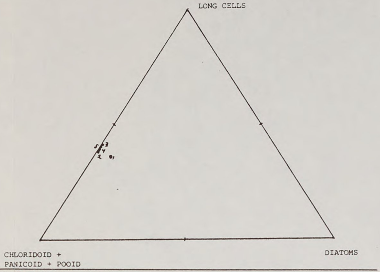
Alvars lacking these dominants



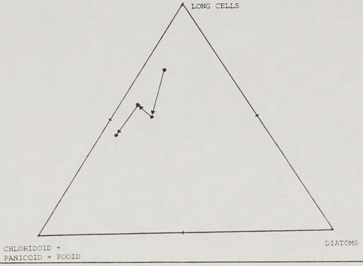
28/33-1 Transect #1



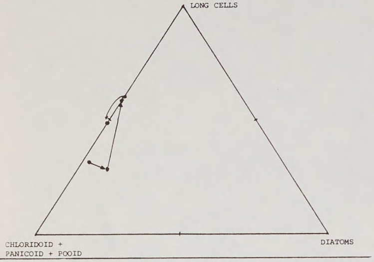
34-1 East Transect



West Road Transect



34-1 North Transect



east transect, whereas the diagram representing 28/33-1 trans. #1 shows considerable oscillation in the relationship between long cells and combined silica cells. In addition, the west road transect and 34-1 north both show unique trends in the silica cell-long cell relationship. If more was known regarding variability among the grass species of the ratio between long cell phytoliths and silica cell phytoliths then a meaningful interpretation of these results might be possible. This figure then is an example of a combination of morphologies that is rather uninformative.

In this discussion several sets of ternary diagrams have been presented to illustrate some trends in the opal phytolith data that are not readily apparent in the data table. These diagrams help to demonstrate the differences in the phytolith assemblages in the soils from the two groups of alvar sites. In addition, they illustrate a number of different patterns of vegetation change in the alvar-forest upland transitions. These conclusions will be summarized in the following section.

SUMMARY.

The following conclusions are drawn from the analysis of the opal phytolith deposits in the soils.

1) The alvar sites that lack *Sporobolus heterolepis* and *Schizachyrium scoparium* as dominants have not supported these species as dominants for a relatively long period of time, if ever.

2) The transects generally show less grassland influence, represented in the soils by a decrease in total grass opal, with distance into the forest. Each transect demonstrates unique details with respect to changes in opal phytolith content with distance into the forest. These details are the combined result of both differences in vegetation history between the transects and random variability of the opal content of the samples.

3) The opal phytolith assemblages in the transition soils are generally quite similar to those in the soils of the *Sporobolus* and *Schizachyrium* dominated alvars, with regard to the proportional relationships between the phytolith morphologies. This is interpreted to suggest some degree of influence of this grassland community in the upland transitions examined.

4) Transects 34-1 east and 28/33-1 trans #1 are located in transitions that appear to be relatively more stable, as compared to the other two transects.

5) From these conclusions and the results of the aerial photograph study it is concluded that there must be a band

or zone that the upland transition can occupy. The position of the transition oscillates and is likely dependent on climatic cycles involving drought and fire. The degree of importance of fire is not known, though it has been recorded historically and is evidenced by charcoal fragments in the soils.

6) Finally it is concluded that ternary diagrams can serve to illustrate trends in the opal phytolith data that are not evident in the data table.

Suggestions for further work that is needed to make opal phytolith deposits of greater utility paleoecologically.

The following areas need to be investigated further so that opal phytoliths will be of greater utility in paleoecological studies.

1) Differential production rates of phytoliths between taxa.
2) Differential weathering rates between different sizes of phytoliths.

3) Variability of opal phytolith deposits within a site, perhaps as it relates to microtopographic variations.
4) The significance of the long cell : silica cell phytolith ratio and variability between taxa.
5) Finally, developing a greater understanding of the capacity of phytolith deposits to discern different plant communities, perhaps through comparisons of similarity calculations of vegetation types with similarity calculations of opal phytolith deposits.

The Maxton Plains is an ideal setting for investigation of these areas because of the limited flora, the shallow soils and the lack of forest influence in the central part of the alvar sites.

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Appendix A

Figure 16 Map of the state of Michigan.

Figure 17. Main map of the Maxton Plains of Drummond Island.


Maxton Plains
DRUMMOND ISLAND
Poe Point
Chippewa Point
Grand Marias Lake
Dawson Lake
Bruce Pt.
Raynolds Point
Paw Point
Colton Bay
R.6E.
R.7E.
T.43N.
T.42N.
20
21
22
23
26
25
30
29
28
27
30
29
31
32
33
34
35
36
31
32
3
2
1
6
5
A
B
C
D
E
Alvar
Marsh
Forest
Small lakes
Kilometers
0
.5
1.0
0
.5
1.0
Miles
Transects
A= Transect 34-1 East
B= Transect 34-1 North
C= West Road Transect
D= 28/33-1 Trans. #1
E= 28/33-1 Trans. #2

Figure 18. Map of the Maxton Plains with site numbers.

Sites studied in 1983 for vegetation composition

28/29-1
28/33-1
29-2
33-2
33-4
34-1
34-2
34-3
34-5
36-6
36/31-1

APPENDIX B. A checklist of the taxa found on the Maxton Plains alvars

EQUISETOPHYTA

Equisetaceae
  Equisetum arvense L.

POLYPODIOPHYTA
OPHIOGLOSSIDAE

Ophioglossaceae
  Botrychium simplex E.Hitchc.

POLYPODIIDAE

Cyatheaceae
  Pteridium aquilinum (L.)Kuhn. var. *latiusculum* (Desv.) Underw.

PINOPHYTA
PINIDAE

Pinaceae
  Picea glauca (Moench) Voss

Cupressaceae
  Juniperus communis L.
  J. horizontalis Moench
  Thuja occidentalis L.

MAGNOLIOPHYTA
MAGNOLIIDAE

Ranunculaceae
  Anemone canadensis L.
  Aquiligia canadensis L. var. *hybrida* Hook.
  Ranunculus acris L.
  R. fascicularis Muhl.

CARYOPHYLLIDAE

Caryophyllaceae
  Arenaria serpyllifolia L.
  A.stricta Michx.
  Cerastium arvense L.
  Silene antirrhina L.

Polygonaceae
  Rumex crispus L.

DILLENIDAE

Clusiaceae
  Hypericum kalmianum L.
  H. perforatum L.

Violaceae
  Viola nephrophylla Greene

Salicaceae
  Populus tremuloides Michx.

Brassicaceae
  Arabis hirsuta (L.) Scop. var. *pycnocarpa* (Hopkins) Rollins
  Barbarea vulgaris R.Br.
  Cardamine parviflora L. var. *arenicola* (Britt.) O.E. Schulz.
  Erucastrum gallicum (Willd.) O.E. Schulz.

Ericaceae
  Arctostaphylos uva-ursi (L.) Spreng.

ROSIDAE

Grossulariaceae
  Ribes oxyacanthoides L.

Saxifragaceae
  Saxifraga virginiensis Michx. (=*S. nivalis* L. ?)

Rosaceae
  Amelanchier sanguinea (Pursh) DC.
  Fragaria virginiana Duchesne
  Geum triflorum Pursh.
  Potentilla anserina L.
  P. fruticosa L.
  P. norvegica L.
  P. recta L.
  Prunus virginiana L.
  P. pumila L. var. *depressa* (Pursh.) Gl.
  Rosa acicularis Lindl.
  R. blanda Ait.

Fabaceae
  Lathyrus palustris L.
  Medicago lupulina L.
  Trifolium hybridum L.
  T. pratense L.
  T. repens L.
  Vicia americana Muhl.

Eleagnaceae
  Shepherdia canadensis (L.) Nutt.

Onegraceae
  Epilobium ciliatum Raf.

Santalaceae
  Comandra umbellata (L.) Nutt.

Vitaceae
  Vitis riparia Michx.

Polygalaceae
  Polygala senega L.

Anacardiaceae
- *Rhus aromatica* Ait.
- *R. glabra* L.

Geraniaceae
- *Geranium bicknellii* Britt.
- *G. carolinianum* L.

Apiaceae
- *Daucus carota* L.

ASTERIDAE

Apocynaceae
- *Apocynum androsaemifolium* L.
- *A. sibiricum* Jacq. var.*cordigerum* (Greene) Fern.

Verbenaceae
- *Verbena simplex* Lehm.

Lamiaceae
- *Prunella vulgaris* L. var. *lanceolata* (Bart.) Fern.
- *Satureja glabella* (Michx.) Briquet var. *angustifolia* (Torr.) Svenson
- *Scutellaria parvula* Michx.
- *Trichostema brachiatum* L.

Scrophulariaceae
- *Castilleja coccinea* (L.) Spreng.
- *Verbascum thapsus* L.
- *Veronica arvensis* L.
- *V. peregrina* L. var. *xalapensis* (HBK) St. John & Warren

Campanulaceae
- *Campanula rotundifolia* L.

Plantaginaceae
- *Plantago lanceolata* L.

Caprifoliaceae
- *Symphoricarpos albus* (L.) Blake

Asteraceae
- *Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper
- *Ambrosia artemisiifolia* L.
- *Antennaria neglecta* Greene
- *Artemisia campestris* L. ssp. *caudata* (Michx.) Hall & Clem.
- *Aster ciliolatus* Lindl.
- *A. pilosus* Wild. var. *pringlei* (Gray) Blake
- *A. ptarmicoides* (Nees) T. & G.
- *Centaurea maculosa* Lam.
- *Chrysanthemum leucanthemum* L.
- *Hieracium aurantiacum* L.
- *H. piloselloides* Vill. (=*H. florentinum* All., *H. caespitosa* Dumort., *H. pratense* Tausch., *H. praealtum* Gochnat, *H. floribundum* Wimmer & Grab. see Voss and Bohlke 1978)

Cirsium arvense (L.) Scop.
C. hillii (Canbyi) Fern.
Senecio pauperculus Michx.
Solidago canadensis L.
S. nemoralis Ait.
S. ohioensis Riddell.
Taraxacum officinale Weber
Tragopogon pratensis L.

ALISMATIDAE

Juncaginaceae
Triglochin maritima L.

COMMELINIDAE

Juncaceae
Juncus dudleyi Weig.

Poaceae
Agropyron trachycaulum (Link) Malte (= *A. caninum* Linn.?)
Agrostis gigantea Roth.
A. hyemalis (Walter) BSP.
Bromus kalmii Gray
Danthonia cespitosa (L.) Beauv.
Dichanthelium acuminatum (Schwartz) Gould & Clark (=*Panicum implicatum* Schribner, *P. lindheimeri* Nash)
Festuca ovina L. var. *saximontana* (Rydb.) Gl.
Glyceria striata (Lam.) Hitchc.
Phleum pratense L.
Poa compressa L.
P. pratense L.
Schizachyrium scoparium (Michx.) Nash
Sporobolus heterolepis Gray
Trisetum spicatum (L.) Richter var. *molle* (Michx.) Beal

Cyperaceae
Carex castanea Wahl.
C. crawei Dew.
C. garberi Fern.
C. interior Bailey
C. laxiflora Lam.
C. merritt-fernaldii Mackenz.
C. richardsonii R.Br.
C. scirpoidea Michx.
C. umbellata Schkuhr.
C. viridula Michx.
Eleocharis compressa Sulliv.

LILIIIDAE

Liliaceae
Lilium philadelphicum L.
Smilacina stellata (L.) Desf.
Zigadenus glaucus Nutt.

Iridaceae
Sisyrinchium montanum Greene

Appendix C. Alphabetical listing of species encountered on the alvars of the Maxton Plains.

Achillea millefolium ssp. _lanulosa_ *
Agropyron trachycaulum *
Agrostis hyemalis
Agrostis gigantea
Ambrosia artemisiifolia
Amelanchier sanguinea *
Anemone canadensis
Antennaria neglecta
Apocynum androsaemifolium
Apocynum sibiricum var. _cordigerum_
Aquilegia canadensis var. _hybrida_
Arabis hirsuta var. _pycnocarpa_
Arctostaphylos uva-ursi
Arenaria serpyllifolia
Arenaria stricta
Artemisia campestris ssp. _caudata_ *
Aster ciliolatus
Aster pilosus var. _pringlei_
Aster ptarmicoides *
Barbarea vulgaris
Botrychium simplex
Bromus kalmii *
Campanula rotundifolia
Cardamine parviflora var. _arenicola_
Carex castanea
Carex crawei *
Carex eburnea *
Carex garberi *
Carex interior
Carex laxiflora
Carex merritt-fernaldii
Carex richardsonii
Carex scirpoidea *
Carex umbellata *
Carex viridula
Castilleja coccinea
Centaurea maculosa
Cerastium arvense
Chrysanthemum leucanthemum
Cirsium arvense
Cirsium hillii
Comandra umbellata *
Danthonia spicata *
Daucus carota
Deschampsia cespitosa *
Dichanthelium acuminatum
Eleocharis compressa *
Equisetum arvense *
Epilobium ciliatum
Erucastrum gallicum
Festuca ovina var. _saximontana_ *
Fragaria virginiana *

Appendix C (continued)

Geranium bicknellii
Geranium carolinianum
Geum triflorum
Glyceria striata
Hieracium aurantiacum
Hieracium piloselloides
Hypericum kalmianum
Hypericum perforatum
Juncus dudleyi *
Juniperus communis *
Juniperus horizontalis *
Lathyrus palustris
Lilium philadelphicum
Medicago lupulina
Phleum pratense
Picea glauca *
Plantago lanceolata
Poa compressa *
Poa pratensis *
Populus tremuloides *
Polygala senega
Potentilla anserina
Potentilla fruticosa
Potentilla norvegica
Potentilla recta
Prunella vulgaris var. *lanceolata*
Prunus pumila var. *depressa* *
Prunus virginiana *
Pteridium aquilinum var. *latiusculum*
Ranunculus acris
Ranunculus fascicularis
Rhus aromatica
Rhus glabra
Ribes oxyacanthoides
Rosa acicularis
Rosa blanda
Rumex crispus
Satureja glabella var. *angustifolia*
Satureja vulgaris
Saxifraga virginiensis
Schizachyrium scoparium *
Scutellaria parvula
Senecio pauperculus *
Shepherdia canadensis *
Silene antirrhina
Sisyrinchium montanum
Smilacina stellata
Solidago canadensis *
Solidago nemoralis
Solidago ohioensis
Sporobolus heterolepis *
Sporobolus vaginiflorus *
Symphoricarpos albus *

Appendex C (continued)

Taraxacum officinale
Thuja occidentalis *
Tragopogon pratensis
Trichostema brachiatum
Trifolium hybridum
Trifolium pratense
Trifolium repens
Triglochin maritima
Trisetum spicatum var. *molle*
Verbascum thapsus
Verbena simplex
Veronica arvensis
Veronica peregrina
Vicia americana
Viola nephrophylla
Vitis riparia
Zigadenus glaucus *

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* Indicates species that were prepared for opal phytolith reference materials.

APPENDIX D

Results of vegetation sampling.

Table 12. Results of vegetation sampling for site 28/29-1.

Site 28/29-1

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	36.7	93.3	42.0	14.1	56.1	1
Eleocharis compressa	18.8	60.0	21.5	9.1	30.6	2
Senecio pauperculus	7.6	90.0	8.7	13.6	22.3	3
Poa compressa	5.4	73.3	6.2	11.1	17.3	4
Hieracium piloselloides	2.3	53.3	2.6	8.1	10.7	5
Schizachyrium scoparium	4.1	23.3	4.7	3.5	8.2	6
Agropyron trachycaulum	1.3	36.7	1.4	5.6	7.0	7
Carex umbellata	2.3	23.3	2.7	3.5	6.2	8
Ambrosia artemisiifolia	.3	26.7	.3	4.0	4.3	9
Achillea millefolium	1.0	16.7	1.1	2.5	3.6	10
Carex crawei	1.7	6.7	1.9	1.0	2.9	11
Phleum pratense	.5	13.3	.5	2.0	2.5	12
Campanula rotundifolia	.4	13.3	.4	2.0	2.4	13
Aster ptarmicoides	.5	10.0	.5	1.5	2.0	14
Bromus kalmii	.3	10.0	.4	1.5	1.9	15
Scutellaria parvula	.3	10.0	.3	1.5	1.8	16
Fragaria virginiana	.6	6.7	.7	1.0	1.7	17
Geranium carolinianum	.2	10.0	.2	1.5	1.7	17
Danthonia spicata	.4	6.7	.5	1.0	1.5	18
Carex garberi	.4	6.7	.5	1.0	1.5	18
Juniperus communis	.4	6.7	.4	1.0	1.4	19
Juncus dudleyi	.2	6.7	.2	1.0	1.2	20
Deschampsia cespitosa	.1	6.7	.2	1.0	1.2	20
Ranunculus fascicularis	.1	6.7	.1	1.0	1.1	21
Botrichium simplex	.1	6.7	.1	1.0	1.1	21
Veronica arvensis	.1	6.7	.1	1.0	1.1	21
Taraxacum officinale	.1	6.7	.1	1.0	1.1	21
Carex richardsonii	.5	3.3	.5	.5	1.0	22
Poa pratensis	.4	3.3	.5	.5	1.0	22
Geum triflorum	.3	3.3	.3	.5	.8	23
Dichanthelium accuminatum	.1	3.3	.1	.5	.6	24
Lathyrus palustris	.1	3.3	.1	.5	.6	24
Castilleja coccinea	<.1	3.3	0.0	.5	.5	25
Arenaria stricta	<.1	3.3	0.0	.5	.5	25
	87.6	660.0	99.8	99.6	199.4	

Table 13. Results of vegetation sampling for site 28/33-1.

Site 28/33-1

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	42.8	96.7	44.1	11.8	55.9	1
Poa compressa	8.4	93.3	8.6	11.4	20.0	2
Senecio pauperculus	6.5	86.7	6.7	10.6	17.3	3
Eleocharis compressa	10.3	53.3	10.6	6.5	17.1	4
Hieracium piloselloides	3.4	76.7	3.5	9.4	12.9	5
Agropyron trachycaulum	3.8	73.3	3.9	8.9	12.8	6
Fragaria virginiana	6.0	36.7	6.2	4.5	10.7	7
Achillea millefolium	2.5	30.0	2.6	3.7	6.3	8
Carex umbellata	2.4	26.7	2.4	3.3	5.7	9
Phleum pratense	1.6	16.7	1.7	2.0	3.7	10
Scutellaria parvula	.4	26.7	.4	3.3	3.7	10
Ranunculus fascicularis	.4	23.3	.4	2.8	3.2	11
Ambrosia artemisiifolia	.3	23.3	.3	2.8	3.1	12
Bromus kalmii	1.1	13.3	1.1	1.6	2.7	13
Schizachyrium scoparium	1.3	10.0	1.4	1.2	2.6	14
Botrichium simplex	.2	20.0	.2	2.4	2.6	14
Deschampsia cespitosa	.9	13.3	.9	1.6	2.5	15
Hypericum perforatum	.6	13.3	.6	1.6	2.2	16
Carex crawei	1.0	6.7	1.0	.8	1.8	17
Taraxacum officinale	.2	13.3	.2	1.6	1.8	17
Poa pratensis	.6	6.7	.6	.8	1.4	18
Carex richardsonii	.5	6.7	.5	.8	1.3	19
Carex garberi	.4	6.7	.4	.8	1.2	20
Cerastium arvense	.2	6.7	.2	.8	1.0	21
Geranium carolinianum	.1	6.7	.1	.8	.9	22
Danthonia spicata	.3	3.3	.3	.4	.7	23
Carex merritt-fernaldii	.2	3.3	.2	.4	.6	24
Juniperus communis	.2	3.3	.2	.4	.6	24
Aster ptarmicoides	.2	3.3	.2	.4	.6	24
Juncus dudleyi	.1	3.3	.1	.4	.5	25
Smilacina stellata	.1	3.3	.1	.4	.5	25
Dichanthelium acuminatum	.1	3.3	.1	.4	.5	25
Sisyrinchium montanum	.1	3.3	.1	.4	.5	25
Lathyrus palustris	.1	3.3	.1	.4	.5	25
Castilleja coccinea	<.1	3.3	0.0	.4	.4	26
	97.3	819.8	100.0	99.8	199.8	

Table 14. Results of vegetation sampling for site 29-2.

Site 29-2

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	46.9	96.7	43.3	14.3	57.6	1
Eleocharis compressa	22.3	83.3	20.6	12.3	32.9	2
Senecio pauperculus	14.0	90.0	12.9	13.3	26.2	3
Poa compressa	10.6	96.7	9.8	14.3	24.1	4
Hieracium piloselloides	1.8	40.0	1.7	5.9	7.6	5
Hypericum perforatum	1.5	36.7	1.4	5.4	6.8	6
Ambrosia artemisiifolia	1.1	33.3	1.0	4.9	5.9	7
Ranunculus fascicularis	.8	33.3	.7	4.9	5.6	8
Danthonia spicata	2.0	20.0	1.8	3.0	4.8	9
Geranium carolinianum	.4	20.0	.3	3.0	3.3	10
Cerastium arvense	.7	16.7	.7	2.5	3.2	11
Carex crawei	1.4	10.0	1.3	1.5	2.8	12
Scutellaria parvula	.9	13.3	.8	2.0	2.8	12
Fragaria virginiana	.6	13.3	.5	2.0	2.5	13
Botrichium simplex	.1	13.3	.1	2.0	2.1	14
Schizachyrium scoparium	.7	6.7	.7	1.0	1.7	15
Carex umbellata	.7	6.7	.6	1.0	1.6	16
Juniperus communis	.4	6.7	.4	1.0	1.4	17
Epilobium ciliatum	.3	6.7	.3	1.0	1.3	18
Taraxacum officinale	.2	6.7	.2	1.0	1.2	19
Prunella vulgaris	.2	3.3	.2	.5	.7	20
Sisyrinchium montanum	.1	3.3	.1	.5	.6	21
Veronica arvensis	.1	3.3	.1	.5	.6	21
Agropyron trachycaulum	.1	3.3	.1	.5	.6	21
Bromus kalmii	.1	3.3	.1	.5	.6	21
Phleum pratense	.1	3.3	.1	.5	.6	21
Juncus dudleyi	.1	3.3	.1	.5	.6	21
Polygala senega	<.1	3.3	0.0	.5	.5	22
	108.2	676.5	99.9	100.3	200.2	

Table 15. Results of vegetation sampling for site 33-2.

Site 33-2

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	25.7	100.0	37.4	13.4	50.8	1
Schizachyrium scoparium	8.8	43.3	12.8	5.8	18.6	2
Eleocharis compressa	4.6	40.0	6.7	5.4	12.1	3
Poa compressa	2.8	60.0	4.1	8.0	12.1	3
Carex crawei	4.0	43.3	5.8	5.8	11.6	4
Fragaria virginiana	2.9	53.3	4.2	7.1	11.3	5
Danthonia spicata	2.3	53.3	3.3	7.1	10.4	6
Senecio pauperculus	1.4	60.0	2.1	8.0	10.1	7
Hypericum perforatum	2.1	33.3	3.1	4.5	7.6	8
Hieracium piloselloides	1.5	36.7	2.1	4.9	7.0	9
Agropyron trachycaulum	1.0	30.0	1.5	4.0	5.5	10
Comandra umbellata	1.3	20.0	1.9	2.7	4.6	11
Carex umbellata	1.8	13.3	2.7	1.8	4.5	12
Carex richardsonii	1.3	16.7	1.9	2.2	4.1	13
Arctostaphylos uva-ursi	1.6	10.0	2.4	1.3	3.7	14
Aster ptarmicoides	.9	16.7	1.4	2.2	3.6	15
Bromus kalmii	.7	16.7	1.0	2.2	3.2	16
Prunella vulgaris	.3	16.7	.5	2.2	2.7	17
Juniperus communis	.9	6.7	1.3	.9	2.2	18
Deschampsia cespitosa	.3	13.3	.4	1.8	2.2	18
Campanula rotundifolia	.3	10.0	.4	1.3	1.7	19
Achillea millefolium	.3	10.0	.4	1.3	1.7	19
Carex scirpoidea	.7	3.3	1.0	.4	1.4	20
Ranunculus fascicularis	.1	10.0	.1	1.3	1.4	20
Polygala senega	.1	6.7	.2	.9	1.1	21
Solidago nemoralis	.4	3.3	.5	.4	.9	22
Amelanchier sanguinea	.2	3.3	.3	.4	.7	23
Aster ciliolatus	.2	3.3	.2	.4	.6	24
Lathyrus palustris	.1	3.3	.1	.4	.5	25
Festuca ovina	<.1	3.3	0.0	.4	.4	26
Sisyrinchium montanum	<.1	3.3	0.0	.4	.4	26
Scutellaria parvula	<.1	3.3	0.0	.4	.4	26
	68.6	746.4	99.8	99.3	199.1	

Table 16. Results of vegetation sampling for site 33-4.

Site 33-4

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	33.7	96.7	45.1	15.1	60.2	1
Eleocharis compressa	16.9	60.0	22.6	9.4	32.0	2
Senecio pauperculus	2.9	76.7	3.9	12.0	15.9	3
Poa compressa	1.4	63.3	1.8	9.9	11.7	4
Hieracium piloselloides	1.9	50.0	2.5	7.8	10.3	5
Carex umbellata	3.1	33.3	4.2	5.2	9.4	6
Agropyron trachycaulum	1.6	36.7	2.2	5.7	7.9	7
Danthonia spicata	1.8	16.7	2.5	2.6	5.1	8
Schizachyrium scoparium	1.7	16.7	2.3	2.6	4.9	9
Scutellaria parvula	.3	26.7	.4	4.2	4.6	10
Ambrosia artemisiifolia	.6	23.3	.8	3.6	4.4	11
Fragaria virginiana	.9	20.0	1.2	3.1	4.3	12
Carex crawei	1.4	13.3	1.8	2.1	3.9	13
Aster ptarmicoides	.6	13.3	.8	2.1	2.9	14
Juniperus communis	1.4	6.7	1.8	1.0	2.8	15
Deschampsia cespitosa	.9	10.0	1.2	1.6	2.8	15
Aster pilosus	.4	13.3	.6	2.1	2.7	16
Carex garberi	1.6	3.3	2.1	.5	2.6	17
Comandra umbellata	.2	10.0	.3	1.6	1.9	18
Geranium carolinianum	.1	10.0	.1	1.6	1.7	19
Rosa acicularis	.4	6.7	.5	1.0	1.5	20
Taraxacum officinale	.1	6.7	.1	1.0	1.1	21
Achillea millefolium	.4	3.3	.5	.5	1.0	22
Campanula rotundifolia	.3	3.3	.4	.5	.9	23
Arenaria stricta	.1	3.3	.1	.5	.6	24
Bromus kalmii	<.1	3.3	0.0	.5	.5	25
Epilobium ciliatum	<.1	3.3	0.0	.5	.5	25
Ranunculus fascicularis	<.1	3.3	0.0	.5	.5	25
Hypericum perforatum	<.1	3.3	0.0	.5	.5	25
Hieracium auranticum	<.1	3.3	0.0	.5	.5	25
	74.7	639.8	99.8	99.8	199.6	

Table 17. Results of vegetation sampling for site 34-1.

Site 34-1	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	18.1	65.6	25.7	10.1	35.8	1
Poa compressa	4.4	56.2	6.3	8.6	14.9	2
Schizachyrium scoparium	5.4	31.2	7.7	4.8	12.5	3
Carex scirpoidea	4.4	40.6	6.2	6.2	12.4	4
Juniperus horizontalis	7.0	12.5	10.0	1.9	11.9	5
Eleocharis compressa	5.4	28.1	7.6	4.3	11.9	5
Senecio pauperculus	2.4	50.0	3.4	7.7	11.1	6
Danthonia spicata	3.2	40.6	4.5	6.2	10.7	7
Hieracium piloselloides	1.7	40.6	2.3	6.2	8.5	8
Arctostaphylos uva-ursi	3.4	15.6	4.8	2.4	7.2	9
Prunus pumila	1.7	18.8	2.4	2.9	5.3	10
Comandra umbellata	1.0	25.0	1.4	3.8	5.2	11
Aster pilosus	1.3	18.8	1.9	2.9	4.8	12
Agropyron trachycaulum	.9	15.6	1.3	2.4	3.7	13
Artemisia campestris	.9	15.6	1.2	2.4	3.6	14
Arenaria stricta	1.0	12.5	1.4	1.9	3.3	15
Fragaria virginiana	1.0	12.5	1.4	1.9	3.3	15
Hypericum perforatum	.9	12.5	1.3	1.3	3.2	16
Campanula rotundifolia	.7	12.5	1.0	1.9	2.9	17
Ambrosia artemisiifolia	.1	12.5	.2	1.9	2.1	18
Taraxacum officinale	.1	12.5	.1	1.9	2.0	19
Carex crawei	.6	6.2	.9	1.0	1.9	20
Bromus kalmii	.3	9.4	.5	1.4	1.9	20
Dichanthelium acuminatum	.5	6.2	.7	1.0	1.7	21
Achillea millefolium	.2	9.4	.3	1.4	1.7	21
Carex merritt-fernaldii	.4	6.2	.6	1.0	1.6	22
Prunella vulgaris	.4	6.2	.6	1.0	1.6	22
Solidago nemoralis	.2	6.2	.4	1.0	1.4	23
Potentilla fruticosa	.2	6.2	.3	1.0	1.3	24
Deschampsia cespitosa	.6	6.2	.2	1.0	1.2	25
Rhus aromatica	.4	3.1	.6	.5	1.1	26
Zigadenus glaucus	.3	3.1	.4	.5	.9	27
Cerastium arvense	.2	3.1	.3	.5	.8	28
Juniperus communis	.2	3.1	.3	.5	.8	28

Table 17. continued.
Site 34-1 (cont.)

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Carex umbellata	.2	3.1	.2	.5	.7	29
Symphoricarpos albus	.1	3.1	.2	.5	.7	29
Satureja vulgaris	.1	3.1	.2	.5	.7	29
Apocynum androsaemifolium	.2	3.1	.2	.5	.7	29
Phleum pratense	.1	3.1	.1	.5	.6	30
Aster ptarmicoides	.1	3.1	.1	.5	.6	30
Equisetum arvense	<.1	3.1	0.0	.5	.5	31
Castilleja coccinea	<.1	3.1	0.0	.5	.5	31
	70.2	682.9	100.1	99.9	200.0	

Table 18. Results of vegetation sampling for site 34-2.

Site 34-2

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Poa pratensis	24.3	70.0	22.1	7.7	29.8	1
Fragaria virginiana	16.4	90.0	14.9	9.9	24.8	2
Trifolium hybridum	15.8	60.0	14.4	6.6	21.0	3
Hieracium piloselloides	8.1	100.0	7.4	11.0	18.4	4
Phleum pratense	7.0	90.0	6.4	9.9	16.3	5
Poa compressa	7.7	50.0	7.0	5.5	12.5	6
Comandra umbellata	4.9	60.0	4.5	6.6	11.1	7
Chrysanthemum leucanthemum	3.3	70.0	3.0	7.7	10.7	8
Rosa acicularis	1.8	40.0	1.6	4.4	6.0	9
Arenaria serpyllifolia	2.5	30.0	2.3	3.3	5.6	10
Symphoricarpos albus	2.5	30.0	2.3	3.3	5.6	10
Prunella vulgaris	1.9	30.0	1.7	3.3	5.0	11
Solidago canadensis	4.2	10.0	3.8	1.1	4.9	12
Achillea millefolium	1.3	30.0	1.2	3.3	4.5	13
Apocynum androsaemifolium	1.2	30.0	1.1	3.3	4.4	14
Hypericum perforatum	1.5	20.0	1.4	2.2	3.6	15
Campanula rotundifolia	1.3	20.0	1.2	2.2	3.4	16
Taraxacum officinale	.5	20.0	.5	2.2	2.7	17
Aster ciliolatus	1.1	10.0	1.0	1.1	2.1	18
Amelanchier sanguinea	1.0	10.0	.9	1.1	2.0	19
Medicago lupulina	.6	10.0	.5	1.1	1.6	20
Geranium carolinianum	.4	10.0	.4	1.1	1.5	21
Satureja vulgaris	.3	10.0	.3	1.1	1.4	22
Danthonia spicata	.2	10.0	.2	1.1	1.3	23
	109.8	910.0	100.1	100.1	200.2	

Table 19. Results of vegetation sampling for site 34-3.

Site 34-3

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Danthonia spicata	17.1	86.7	15.5	7.3	22.8	1
Hieracium piloselloides	12.2	100.0	11.1	8.4	19.5	2
Fragaria virginiana	11.1	100.0	10.1	8.4	18.5	3
Arctostaphylos uva-ursi	15.1	40.0	13.7	3.4	17.1	4
Poa pratensis	8.5	93.3	7.8	7.8	15.6	5
Achillea millefolium	6.9	73.3	6.3	6.1	12.4	6
Comandra umbellata	4.9	80.0	4.5	6.7	11.2	7
Hieracium auranticum	4.5	80.0	4.1	6.7	10.8	8
Poa compressa	5.2	60.0	4.7	5.0	9.7	9
Chrysanthemum leucanthemum	4.0	66.7	3.6	5.6	9.2	10
Phleum pratense	3.1	53.3	2.9	4.5	7.4	11
Agropyron trachycaulum	1.8	46.7	1.6	3.9	5.5	12
Satureja vulgaris	1.3	46.7	1.2	3.9	5.1	13
Aster ciliolatus	2.3	33.3	2.1	2.8	4.9	14
Campanula rotundifolia	1.8	33.3	1.6	2.8	4.4	15
Prunella vulgaris	1.0	33.3	.9	2.8	3.7	16
Trifolium hybridum	2.6	13.3	2.4	1.1	3.5	17
Hypericum perforatum	.8	33.3	.7	2.8	3.5	17
Medicago lupulina	2.2	13.3	2.0	1.1	3.1	18
Symphoricarpos albus	.7	20.0	.7	1.7	2.4	19
Bromus kalmii	.6	20.0	.5	1.7	2.2	20
Carex umbellata	.7	13.3	.6	1.1	1.7	21
Anemone canadensis	.4	13.3	.4	1.1	1.5	22
Arenaria serpyllifolia	.1	13.3	.1	1.1	1.2	23
Agrostis gigantea	.6	6.7	.5	.6	1.1	24
Populus tremuloides	.1	6.7	.1	.6	.7	25
Cerastium arvense	.1	6.7	.1	.6	.7	25
Taraxacum officinale	.1	6.7	.1	.6	.7	25
	109.8	1193.3	99.9	100.2	200.1	

Table 20. Results of vegetation sampling for site 34-5.

Site 34-5

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	23.6	86.7	33.2	11.7	44.9	1
Hieracium piloselloides	5.1	66.7	7.2	9.0	16.2	2
Carex scirpoidea	8.1	33.3	11.4	4.5	15.9	3
Hypericum perforatum	5.5	50.0	7.7	6.7	14.4	4
Schizachyrium scoparium	5.0	46.7	7.0	6.3	13.3	5
Poa compressa	3.0	63.3	4.2	8.5	12.7	6
Danthonia spicata	3.7	46.7	5.2	6.3	11.5	7
Agropyron trachycaulum	2.0	46.7	2.9	6.3	9.2	8
Fragaria virginiana	2.5	36.7	3.5	4.9	8.4	9
Carex umbellata	1.8	26.7	2.5	3.6	6.1	10
Campanula rotundifolia	.8	36.7	1.2	4.9	6.1	10
Senecio pauperculus	.9	33.3	1.2	4.5	5.7	11
Comandra umbellata	1.2	23.3	1.7	3.1	4.8	12
Arenaria stricta	1.1	23.3	1.5	3.1	4.6	13
Apocynum androsaemifolium	.7	16.7	.9	2.2	3.1	14
Prunus pumila	1.2	10.0	1.6	1.3	2.9	15
Cerastium arvense	.4	16.7	.6	2.2	2.8	16
Arctostaphylos uva-ursi	1.1	6.7	1.5	.9	2.4	17
Aster ptarmicoides	.6	10.0	.8	1.3	2.1	18
Carex richardsonii	.4	6.7	.6	.9	1.5	19
Bromus kalmii	.2	10.0	.2	1.3	1.5	19
Symphoricarpos albus	.6	3.3	.9	.4	1.3	20
Rhus aromatica	.5	3.3	.7	.4	1.1	21
Rosa acicularis	.1	6.7	.1	.9	1.0	22
Eleocharis compressa	.3	3.3	.4	.4	.8	23
Amelanchier sanguinea	.2	3.3	.3	.4	.7	24
Juniperus horizontalis	.2	3.3	.2	.4	.6	25
Juniperus communus	.1	3.3	.1	.4	.5	26
Tragopogon pratensis	.1	3.3	.1	.4	.5	26
Achillea millefolium	.1	3.3	.1	.4	.5	26
Deschampsia cespitosa	<.1	3.3	0.0	.4	.4	27
Scutellaria parvula	<.1	3.3	0.0	.4	.4	27
Ranunculus fascicularis	<.1	3.3	0.0	.4	.4	27
Potentilla fruticosa	<.1	3.3	0.0	.4	.4	27
	71.1	743.2	99.5	99.2	198.7	

Table 21. Results of vegetation sampling for site 36-6.

Site 36-6

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Fragaria virginiana	17.4	90.0	23.4	12.3	35.7	1
Poa compressa	9.8	100.0	13.2	13.7	26.9	2
Chrysanthemum leucanthemum	6.8	90.0	9.1	12.3	21.4	3
Senecio pauperculus	6.8	90.0	9.1	12.3	21.4	3
Hieracium piloselloides	8.3	60.0	11.2	8.2	19.4	4
Hypericum perforatum	6.5	70.0	8.7	9.6	18.3	5
Phleum pratense	3.1	40.0	4.2	5.5	9.7	6
Prunella vulgaris	3.1	40.0	4.2	5.5	9.7	6
Achillea millefolium	2.0	30.0	2.7	4.1	6.8	7
Poa pratensis	2.8	20.0	3.8	2.7	6.5	8
Carex richardsonii	1.5	20.0	2.0	2.7	4.7	9
Amelanchier humilis	2.0	10.1	2.7	1.4	4.1	10
Danthonia spicata	1.0	10.0	1.3	1.4	2.7	11
Carex umbellata	.9	10.0	1.2	1.4	2.6	12
Taraxacum officinale	.9	10.0	1.2	1.4	2.6	12
Agropyron trachycaulum	.6	10.0	.8	1.4	2.2	13
Aster pilosus	.6	10.0	.8	1.4	2.2	13
Rosa acicularis	.2	10.0	.3	1.4	1.7	14
Comandra umbellata	.1	10.0	.1	1.4	1.5	15
	74.4	730.0	100.0	100.1	200.1	

Table 22. Results of vegetation sampling for site 36/31-1.

Site 36/31-1

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Sporobolus heterolepis	21.0	46.7	19.2	5.7	24.9	1
Poa compressa	13.6	83.3	12.4	10.2	22.6	2
Senecio pauperculus	11.7	86.7	10.6	10.7	21.3	3
Hieracium piloselloides	7.3	70.0	6.6	8.6	15.2	4
Phleum pratense	6.2	66.7	5.7	8.2	13.9	5
Achillea millefolium	6.3	56.7	5.8	7.0	12.8	6
Cerastium arvense	4.2	53.3	3.9	6.6	10.5	7
Aster pilosus	4.5	26.7	4.1	3.3	7.4	8
Fragaria virginiana	5.0	13.3	4.5	1.6	6.1	9
Poa pratensis	3.3	23.3	3.0	2.9	5.9	10
Agropyron trachycaulum	2.4	30.0	2.2	3.7	5.9	10
Trifolium hybridum	3.5	20.0	3.2	2.5	5.7	11
Carex umbellata	2.4	23.3	2.2	2.9	5.1	12
Eleocharis compressa	4.3	6.7	3.9	.8	4.7	13
Deschampsia cespitosa	1.9	13.3	1.7	1.6	3.3	14
Rosa acicularis	1.3	16.7	1.2	2.1	3.3	14
Aster ptarmicoides	1.2	16.7	1.1	2.1	3.2	15
Ranunculus fascicularis	.4	23.3	.3	2.9	3.2	15
Danthonia spicata	1.7	13.3	1.5	1.6	3.1	16
Carex merritt-fernaldii	.5	16.7	.5	2.1	2.6	17
Arctostaphylos uva-ursi	2.3	3.3	2.1	.4	2.5	18
Arenaria stricta	.4	16.7	.4	2.1	2.5	18
Campanula rotundifolia	.7	13.3	.7	1.6	2.3	19
Comandra umbellata	.6	13.3	.5	1.6	2.1	20
Zigadenus glaucus	.4	10.0	.4	1.2	1.6	21
Prunella vulgaris	.7	6.7	.7	.8	1.5	22
Chrysanthemum leucanthemum	.7	3.3	.6	.4	1.0	23
Taraxacum officinale	.1	6.7	.1	.8	.9	24
Sisyrinchium montanum	.1	6.7	.1	.8	.9	24
Agrostis gigantea	.2	3.3	.2	.4	.6	25
Smilacina stellata	.2	3.3	.2	.4	.6	25
Aster ciliolatus	.1	3.3	.1	.4	.5	26

Table 22. Continued.
Site 36/31-1 (cont.)

	cover	freq.	rel. cover	rel. freq.	imp. val.	rank
Equisetum arvense	.1	3.3	.1	.4	.5	26
Satureja vulgaris	.1	3.3	.1	.4	.5	26
Lathyrus palustris	.1	3.3	.1	.4	.5	26
Hypericum perforatum	<.1	3.3	0.0	.4	.4	27
Artemisia campestris	<.1	3.3	0.0	.4	.4	27
	109.5	813.1	100.0	100.0	200.0	

Appendix E. Table 23. Species lists for sites surveyed in 1984.

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Achillea millefolium ssp. lanulosa	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Agropyron trachycaulum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Agrostis hyemalis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis gigantea	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ambrosia artemisiifolia	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Amelanchier sanguinea	1	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	0
Anemone canadensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Antenaria neglecta	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1
Apocynum androsaemifolium	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	0
Apocynum sibiricum var. cordigerum	0	1	1	1	1	1	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	0	1
Aquelegia canadensis var. hybrida	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1
Arabis hirsuta var. pycnocarpa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Arctostaphylos uva-ursi	0	1	1	0	1	1	0	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1	1	0	1	1	1	1
Arenaria serpyllifolia	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	1	0	0	0
Arenaria stricta	1	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0
Artemisia campestris ssp. caudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Aster ciliolatus	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0
Aster pilosus var. pringlei	1	1	1	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1
Aster ptarmicoides	1	0	1	1	1	1	0	1	1	0	0	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	1	0	1
Barbarea vulgaris	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bromus kalmii	0	1	1	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0
Campanula rotundifolia	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
Cardamine parviflora var. arenicola	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex castanea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Carex crawei	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1
Carex garberi	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Carex interior	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Carex laxiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Carex merritt-fernaldii	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0
Carex richardsonii	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Carex scirpoidea	1	1	1	0	1	1	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Carex umbellata	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Carex viridula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castilleja coccinea	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Centaurea maculosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Cerastium arvense	1	1	0	0	0	0	1	1	1	1	0	0	1	0	1	1	1	1	0	1	1	0	1	1	1	0	0	0	0
Chrysanthemum leucanthemum	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0
Cirsium arvense	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium hillii	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Comandra umbellata	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Danthonia spicata	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Daucus carrota	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia cespitosa	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	1
Dichanthelium accuminatum	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eleocharis compressa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0	1
Equisetum arvense	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0
Epilobium ciliatum	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0
Erucastrum gallicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Festuca ovina var. saximontana	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Fragaria virginiana	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Geranium bicknellii	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Geranium carolinianum	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0
Geum triflorum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyceria striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hieracium aurantiacum	1	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0
Hieracium piloselloides	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Hypericum kalmianum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hypericum perforatum	1	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0
Juncus dudleyi	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Juniperus communis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Juniperus horizontalis	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Lathyrus palustris	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0
Lilium philadelphicum	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Medicago lupulina	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
Phleum pratense	1	1	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Poa compressa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Poa pratensis	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Populus tremuloides	0	0	1	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0
Polygala senega	0	0	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0
Potentilla anserina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla fruticosa	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1
Potentilla norvegica	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0
Potentilla recta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Prunella vulgaris var. lanceolata	0	1	0	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1
Prunus pumila var. depressa	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Prunus virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Pteridium aquilinum var. latiusculum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ranunculus acris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Ranunculus fascicularis	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0

Appendix E. Table 23. Continued

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Rhus aromatica	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	1	1
Rhus glabra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ribes oxyacanthoides	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa acicularis	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0
Rosa blanda	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0
Rumex crispus	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Satureja glabella var. angustifolia	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Satureja vulgaris	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Saxifraga virginiensis	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	1	0	0
Schizachyrium scoparium	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1
Scutellaria parvula	0	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1
Senecio pauperculus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1
Shepherdia canadensis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1
Silene antirrhina	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Sisyrinchium montanum	1	1	1	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1
Smilacina stellata	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0
Solidago canadensis	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
Solidago nemoralis	0	1	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1
Solidago ohioensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Sporobolus heterolepis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0
Symphoricarpos albus	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0	1	0
Taraxacum officinale	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	0	0	0
Thuja occidentalis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tragopogon pratensis	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
Trichostema brachiatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Trifolium hybridum	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0
Trifolium pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Trifolium repens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
Triglochin maritima	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trisetum spicatum var. molle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Verbascum thapsus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Verbena simplex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Veronica arvensis	1	0	1	0	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0
Veronica peregrina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Vicia americana	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Zigadenus glaucus	1	0	0	0	0	0	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0

LEGEND TO SITE NUMBERS

Site 1= 5/6-2
2= 30-2
3= 20-1
4= 20-2
5= 20-3
6= 20-4
7= 27-24
8= 28/29-1
9= 28/33-1
10= 29-2

Site 11= 29-4
12= 32-1
13= 32-5
14= 33-2
15= 33-3
16= 33-4
17= 34-1
18= 34-5
19= 34-2
20= 34-3

Site 21= 34-6
22= 35-7
23= 36/31-1
24= 36-2
25= 36-4
26= 36-5
27= 36-6
28= 36-7
29= 20-8

Appendix F. Notes on the sites surveyed in 1984.

Site	Notes
5/6-2	Appears to be wet for the most part; cutting on edges; poor quality, weedy. Has *sporobolus* and *Schizachyrium* on rise near rocks at north end.
20-1	Very shallow soil, cobbles, some pavement in spots.
20-4	ORV trail through site; some pavement; wet edge.
32-5	Edge near road rather moist.
33-3	ORV trail on south and southeast sides.
35-7	Quite weedy; some aspen in middle of site; south side of road is better.
36-2	Slopes down to north; many down trees; rather weedy.
36-5	Edges are better that middle of site, disturbed.
36-7	Much *Hieracium*; many down trees.
36-6	*Carex* *richardsonii* and *Schizachyrium* around juniper and dead *Picea* in center; most of site weedy.

Appendix G Calculated similarity values.

Table 24. Sorensen index of community similarity calculated for sites examined in 1984

Sorensen's index of community similarity

2	63																											
3	58	73																										
4	55	59	59																									
5	59	64	67	60																								
6	63	63	63	69	68																							
7	72	52	50	53	49	55																						
8	65	65	65	44	58	44	59																					
9	69	59	59	56	57	51	68	78																				
10	70	56	54	55	54	54	69	65	80																			
11	56	62	68	64	73	62	48	50	54	53																		
12	68	56	58	61	51	54	64	60	73	73	46																	
13	65	55	55	61	50	50	70	60	69	70	61	62																
14	70	64	68	60	65	59	63	66	76	68	60	68	66															
15	79	63	61	56	57	53	77	71	83	81	54	77	75	75														
16	72	60	64	60	50	56	68	63	75	77	52	72	72	72	79													
17	69	65	61	54	66	58	59	69	72	65	57	65	62	73	69	68												
18	63	67	65	56	63	59	60	79	75	67	56	65	57	72	67	69	72											
19	44	33	28	25	39	30	38	39	39	44	27	33	25	38	38	33	30	43										
20	55	43	35	40	38	40	53	44	49	49	34	42	37	46	45	48	40	51	71									
21	73	64	62	57	62	58	65	62	65	59	57	58	55	67	68	70	65	68	46	57								
22	61	54	49	38	53	46	58	64	59	55	47	52	41	62	60	58	52	61	51	58	64							
23	82	56	54	49	51	57	67	65	75	73	44	68	59	64	79	72	60	63	51	62	71	61						
24	71	58	58	53	64	55	66	69	76	73	56	69	60	65	77	68	60	67	52	56	72	63	73					
25	75	57	47	48	53	48	68	67	69	61	41	61	58	60	70	67	59	62	44	54	87	65	73	72				
26	58	54	47	43	59	55	56	56	57	56	61	50	49	40	52	59	51	52	58	59	56	69	63	67	57			
27	55	49	41	45	56	41	32	48	49	52	46	43	42	56	56	57	47	47	50	52	53	64	55	58	51	61		
28	47	49	44	32	54	45	51	50	49	42	53	38	36	60	49	46	45	54	51	56	54	73	50	54	49	65	62	
29	47	67	69	52	61	62	34	48	47	42	61	44	45	60	48	43	56	55	22	27	48	43	40	46	37	47	43	50
Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28

Key to site numbers:

site	locality	site	locality	site	locality
1	5/6-2	11	29-4	21	34-6
2	30-2	12	32-1	22	35-7
3	20-1	13	32-5	23	36/31-1
4	20-2	14	33-2	24	36-2
5	20-3	15	33-3	25	36-4
6	20-4	16	33-4	26	36-5
7	27-24	17	34-1	27	36-6
8	28/29-1	18	34-5	28	36-7
9	28/33-1	19	34-2	29	20-8
10	29-2	20	34-3		

Appendix G (continued)

Table 25. Horn's index of community similarity calculated for sites examined in 1983.

Horn's index of community similarity

2	.80									
3	.72	.83								
4	.72	.82	.89							
5	.66	.64	.67	.80						
6	.73	.83	.94	.93	.71					
7	.82	.83	.68	.70	.62	.67				
8	.37	.35	.21	.34	.56	.22	.41			
9	.68	.76	.88	.88	.68	.93	.63	.19		
10	.21	.24	.14	.30	.52	.18	.29	.67	.16	
11	.33	.38	.26	.49	.63	.34	.42	.62	.35	.66
Site	1	2	3	4	5	6	7	8	9	10

Key to site numbers:

site	locality
1	34-1
2	33-2
3	33-4
4	28/33-1
5	36/31-1
6	28/29-1
7	34-5
8	34-3
9	29-2
10	34-2
11	36-6