SPECIES DISTRIBUTIONAL PATTERNS IN DUNE SAND AREAS IN THE GRASSLANDS OF SASKATCHEWAN

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Gary K. Hulett

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INTRODUCTION

Dune sand areas present a complex and variable environment for the growth of plants, especially where erosion or deposition has occurred. The instability of the sand surface, along with other physical conditions imposed by the sand particles (moisture relations, hydrology, nutrient status, etc.), is restrictive in its effect on the vegetation and permits the existence of only those species whose adaptive capabilities allow the efficient utilization of the resources of the habitat. This results in a diverse array of vegetation that is often anomalous to that on surrounding finer-textured soils. This, coupled with the severe economic threat posed by sand areas through erosion, has promoted intensive research on dunes in many parts of the world. Stabilization of dunes that are encroaching upon arable land and the improvement of management practices in dune areas utilized for grazing constitute a major portion of this research. Investigations of this nature require an intimate knowledge of the interactions of the vegetational components and their environment, information that can be best utilized when quantitative measurements have been made as to where a particular species grows, where it attains its greatest success and what factors are responsible for its behavior.

The purpose of this study was to examine species distributions on dune sand in an attempt to explain the interrelations between the plants and their habitat. Although such information is available in

Saskatchewan for soils ranging in texture from clay to sandy loam, there is none concerning dune sand vegetation. This study was initiated in 1959 and continued through 1961. During this time, quantitative data were collected, by various methods, in 101 stands located in two major and two minor study areas selected as representative of the overall dune vegetation in the grasslands of Saskatchewan. One major study area was in the Dundurn sand dunes, approximately 15 miles south of Saskatoon, and the other in the Great Sand Hills, particularly south of Sceptre, Lemsford and Portreeve. The minor study areas, in which only a few stands were located, were near Elbow and north of Webb in Prairie Farm Rehabilitation Administration pastures (Fig. 1).

The areal extent of the two major study areas differs considerably, with the Great Sand Hills (Sceptre area) totalling approximately 425 square miles, but the dunes near Dundurn cover only 170 square miles. The areas exhibit characteristic dune topography consisting of actively eroding and depositing areas along with a variety of stabilized forms. It should be emphasized that the study areas represent only a sample of the total dune environment and that physiographical phenomena, vegetation and factorial gradients, other than those to be described, may exist.

The techniques used in the interpretation of the data, although not new in theory or practice, are being applied for the first time in vegetation in the Canadian Mixed Prairie. It is hoped that, in addition to the primary purpose expressed, the methods will aid future researchers in quantitative studies concerning northern grassland vegetation.

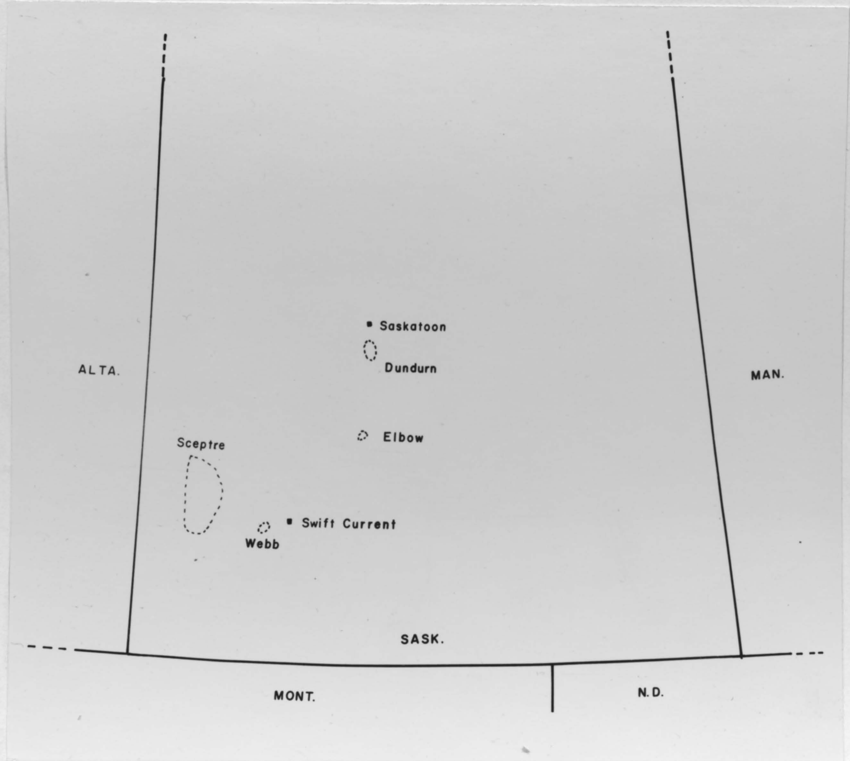

Fig. 1. Outline map of Saskatchewan showing the location of the four study areas.

REVIEW OF LITERATURE

Scientific investigations covering a multitude of practical, geological and ecological aspects have been made on sand dunes. Reclamation work dealing with prevention of dune encroachment upon arable land by planting sand-binding genera, such as Ammophila or Pinus, constitutes a major portion of this research; e.g., Westgate (1904), McLaughlin and Brown (1942), Brown (1948), Chapman (1949), Bennett (1950), Nadeu (1953), Wells (1954), and Davis (1957). The economic value of such work is considerable in areas where there are large dune systems.

A second phase of research that has received much attention is the geomorphological nature of dunes, particularly their development in the absence of vegetation. The physics of blown sand has been described extensively by Bagnold (1935, 1937, and 1954), while Cooper (1958), Ranwell (1958) and Olson (1958a) have described dune development in Oregon, Wales and Michigan. To review the abundant literature dealing with dune geology is beyond the scope and purpose of this paper and therefore, the following references must suffice: Cooper (1935); Smith (1940, 1945, 1949, 1954); Thorp (1952); and Landsberg (1956).

Much research on dunes concerns the nature of the vegetation, particularly the correlation of either species distributional patterns or plant communities with environment. Since the present study involves species behavior in relation to environmental gradients, the major effort of the review will be directed towards studies that are pertinent to this investigation in either causal agents or species similarity. Those studies dealing with sand dunes in grassland regions will be given particular attention, while those concerning forested sand dunes will be mentioned only when particularly significant either in terms of understory species, environment or edaphic development.

Only limited quantitative phytosociological research has been done on sand dunes in Saskatchewan. Most of the work has been qualitative, either on a biotic community basis or as floral descriptions of localized areas. Coupland (1950, 1961) described sand dune vegetation in Saskatchewan as a post-climax tall-grass community. The presence of such vegetation was ascribed to runoff reduction in the porous sand plus lower moisture equivalent, the combination of which resulted in more moisture for plants. Species reported as indicative of pioneer successional stages included: Sporobolus cryptandrus, Oryzopsis hymenoides, Calamovilfa longifolia, Psoralea lanceolata and Helianthus spp. Stabilization of active dunes was considered to change the soil moisture status to a point where Stipa comata became established as the dominant grass. Sedges and shrubs occurred primarily in depressional areas, a distributional pattern that was thought to be related to proximity of the water table to the rooting zone (Coupland 1950). Johnson (1960) studied rooting habits of native prairie plants in dune sand and reported that many dune plants had root systems penetrating to depths of 5 or 6 feet, a morphological characteristic allowing utilization of sub-surface moisture.

The theory has been advanced that compensatory qualities offered by sand dunes allow Boreal Forest species to either project or survive south of the forest border. Picea glauca, for example, is found south of the Boreal Forest on sand dunes (Coupland 1960). Maini (1960) proposed that groves of Populus tremuloides in grassland regions of Saskatchewan are relicts of a forest that covered most of southern Saskatchewan (Kupsch 1960) following the retreat of the last ice sheet from the area. Regardless of origin, dunes do support groves of Populus tremuloides 150 miles southwest of the aspen grove region (Bird 1930; Watts 1960).

Some research has been done on sand dunes in central Alberta, that of Dowding (1929) being the most comprehensive work. The study is mainly qualitative, simply listing various species as occupying particular dune habitats. Odynsky (1958) and Moss (1932), studying parabolic dunes in the same general area, reported that dunes were stabilized by a cover of coarse grass, shrub, aspen, pine and occasional spruce. Similar stabilatory agents were described by Bird (1927) in Manitoba, in an investigation in a transitional area between prairie and forest, where the principal plant communities included: sand plain grasslands and hollows. The latter community resulting from sand erosion almost to the water table supported the growth of trees and shrubs. Bird attributed the vegetational patterns to water table height, noting that good wheat production occurred on sandy soils when the water layer was high, while a fall in the water table decreased production and resulted in severe sand erosion.

Considerable research has been done on species-habitat relationships in certain regions of the United States. These have been mainly in the Great Plains region and along the Pacific and Atlantic coastlines.

One of the best known study areas, in the Great Plains, is the sandhills of Nebraska, an area of particular importance to the present study because of floristic similarities. Rydberg (1895) first described the flora of these sandhills and initiated an era of extensive research in the region by various workers. Pound and Clements (1900), reporting on the various phytogeographical provinces in Nebraska, further described the sandhill region as consisting of two main communities, a bunchgrass formation dominated by Andropogon scoparius, Calamovilfa longifolia, Stipa comata and Sporobolus cryptandrus, and a blowout formation dominated by Psoralea lanceolata and Lygodesmia juncea. No quantitative measures were made of factors causing the distributions, but topography and its interrelated factors were considered important.

Pool (1914), characterized the Nebraska sandhills as regions where moisture conditions were more favorable over those on finer-textured soils, thus permitting growth of plants otherwise absent in the vicinity. He considered the local soil moisture status to be an important factor in affecting species distributions.

Tolstead (1942) studied various environmental factors that were suspected as important in determining vegetational patterns and concluded that the prime causal agent was available soil moisture. Soils of low-lying meadows had a greater organic matter and moisture content than those of bare dunes. Russell and Rhoades (1956) attributed the greater organic matter content in the low-lying areas to water table proximity and contended that all factors associated with organic matter were greater in locations where the water table was near the surface. Tolstead (1942) had also thought this to be important and made detailed measurements of water table fluctuations in various plant communities and found that carices, mesophytic grasses and forbs were common where the water table was near the surface. Germination habits were also found to be important in determining species distribution on blowouts and dunes, since many plants occurring in early stages of succession germinate quickly without a vernalization period (Tolstead 1941).

A recent study in the Nebraska area by Burzlaff (1960) has stressed soil texture as the principal edaphic property affecting vegetational patterns. Significant correlations were found between the range sites of Dyksterhuis (1949), species frequency and various soil properties.

Additional information is available concerning species-habitat interactions in areas adjacent to the Nebraska sandhills. Doell (1938) reported on a dune flora in southwestern Kansas, but no mention was made of causal agents affecting species distribution. Bruner (1931) described stabilized sand dune vegetation in northwestern Oklahoma and reported that woody plants such as Populus and Salix were found only in depressions, a feature that was related to greater amounts of available moisture in such habitats. Ramaley (1938, 1939) and Vestal (1914), working in Colorado, also reported that trees and shrubs were associated with mesic lowland areas, while herbaceous vegetation inhabited the drier dunes. Emerson (1935), working in the White Sands National Monument gypsum dunes, found flat areas between dunes the only habitat with suitable moisture conditions for seedling establishment. Additional research has also been done in New Mexico concerning distributional patterns on sand by Campbell (1929) and McBryde (1933).

A second dune investigation center in the United States is located on the shores of Lake Michigan. The early work is that of H. C. Cowles (1899, 1901), who placed great emphasis on physiography as a factor affecting vegetational distribution and succession on lee and windward dune slopes. Lee slopes were first colonized by grasses and forbs, which were followed in succession by shrubs, such as *Cornus*, *Salix* and *Prunus*. Cowles suggested that with continued humus accumulation, lee slopes and depressions would become more mesic until finally *Acer saccharum* would be the dominant tree. The development of the vegetation on windward slopes was different because of more severe environmental conditions. Initial stabilatory stages consisted of slow invasion by adapted herbaceous plants along with three evergreen species: *Arctostaphylos uva-ursi*, *Juniperus communis*, and *J. horizontalis*.

Topography and exposure were considered important in regulating the species distributions; the former was particularly active in soil and atmospheric moisture level regulation: *i.e.*, slopes and hills were drier than depressions. Wind, however, was considered the chief influence on plant societies, through its ability to modify the physiography. More recently, Olson (1958) has reported vegetation occurring on sand dunes near Lake Michigan as a gradational "climax pattern" as defined by Whittaker (1953). The research by Olson (1958) represents the most intensive work on dunes in North America. The quantitative techniques used in the study yielded information concerning the distinction between vegetal patterns due to autogenic succession (reaction between plants and a particular habitat) and patterns in the vegetation due to differences in habitats.

Working in the same area, Fuller (1912, 1914) studied soil moisture conditions in an active dune community and concluded that, although the habitat appeared xeric, a plentiful supply of moisture existed beneath the dry surface layers of the sand. Xerophytism was attributed to the high evaporative power of the atmosphere. The ability of plants to colonize such xeric habitats has been explained by study of various physiological and morphological adaptations. Whitfield (1932), in California, reported that osmotic concentrations of active dune species were consistently higher than concentrations in species found in stabilized areas and concluded that dunes represent a more xeric habitat, in which a higher diffusion pressure deficit is advantageous in obtaining water. Starr (1912) and Purer (1935, 1936) studied anatomical adaptations in dune plants and found distinct morphological responses to the severe habitat that included: low growth form, long roots, woody stems, thick leaves, evergreen habit, reduced leaves and sunken stomata. All of these modifications imparted low transpiration rates or tolerance to wind erosion. Extensive root systems have also been recorded as habitat adaptations in dune plants by Waterman (1923). Pioneer development on active dunes has been described by Lakela (1939), Buss (1956) and Laing (1958).

Although many workers, Hart and Gleason (1907), Gleason (1910), Vestal (1913), and Shimek (1917), have reported extreme environmental conditions on active dunes (great diurnal temperature fluctuations, intense insolation, low water-retaining and nutrient capacities and shifting substrate), certain portions of the dunes have conditions more favorable for plant growth. Kurz (1923) and Hepburn (1952) found active dune soils alkaline in reaction, low in organic matter, high in calcium carbonate and having high aeration, while with increasing stabilization or in depressional areas the soils became less alkaline, organic content increased and aeration decreased thus providing a more favorable habitat for many species. Similar trends have been reported by Strohecker (1937), Cribbs (1919) and Park (1931). Other workers have considered dune habitat-plant relationships and imparted various factors as causal agents affecting species distribution. These include soil moisture, (McLaughlin 1932; Brown 1950; Marshall 1955) germination habits of species involved, (Gillis 1959), cultural practices (Kilburn 1958), and light (Hicks 1938).

A third prominent study area of dune vegetation exists on the coastlines of the United States. These regions present extensive strands and dunes formed by water deposited and wind blown sand. On the Pacific Coast, most of the work has been in Oregon and Washington (House 1914, 1914a; Couch 1914; and Cooper 1936, 1958), while in southern California, the formation and vegetation of inland crescentic dunes has been described by Rempel (1937).

Atlantic coast ecological work on sand was founded by Harshberger's (1900) report on the strand flora of New Jersey and continued by Olmsted (1937), who described community-habitat relationships in the central lowland of Connecticut and concluded that initial differentiation of the habitats, in which the various plant communities were located, resulted from cultivation and wind erosion of the area in early days of settlement. A more recent study by Martin (1959), of the phytosociological nature of dune vegetation in New Jersey, reported the vegetation and topography as a closely integrated zoned mosaic, in which topography controlled environmental gradients (sand movement, available soil moisture, ground water salinity and salt spray) to which the vegetation responded. Martin emphasized the continuity of both the environmental gradients and the vegetation.

The distribution of vegetation in relation to environmental gradients such as salt spray, nutrients and fire has also been recorded in North and South Carolina (Wells and Shunk 1931; Billings 1938; Wells 1942). Although, the basic factor affecting species distributions in most cases was topography, due to its interrelations with certain factors essential for plant growth (Oosting and Billings 1942; Davis 1942; Oosting 1954).

Laessle (1958), studying sandhill and sand pine scrub vegetation in Florida, concluded that floral contrasts in these communities were due primarily to nutrient differences in the soil that were in turn related to degree of water washing and sorting in original sand deposition.

Extensive work has also been done in Europe concerning species distributional patterns on sand dunes and factors affecting their distribution. The initial work was done by Warming in Denmark (1891, 1909), while recently much research has been done by Salisbury (1952), Webley et al. (1952), Brown (1958), Ranwell (1959) and Willis et al. (1959, 1961), in Great Britain.

Burges et al. (1953) and Rayson (1959) have studied sand dunes in Australia. The latter work, on a single barchan dune in south Australia, reported that four communities were illustrated by the correlation technique of Goodall (1953), but that no clear-cut boundaries existed between the communities. A vegetational continuum concept, connected with a microclimatic gradient present on the dunes, seemed to fit the observed patterns more closely than a discrete unit concept.

DESCRIPTION OF STUDY AREAS

Origin and Nature

A variety of glacial features are exhibited, due to transportation of till and drift by ice and meltwater, in a glaciated area such as Saskatchewan. Sand dunes in Saskatchewan were formed from stratified glacial drift, reworked by the wind into dune forms (Mitchell et al. 1944). The last glacial retreat in Saskatchewan is estimated to have occurred about 10,000 years ago (Kupsch 1960). Upon this retreat, drainage channels were formed to carry the large discharge of meltwater away from the ice. In some cases the channels flowed directly away from the ice, but in most of Saskatchewan, since the inclination of the land is towards Hudson Bay, the meltwater drained towards the retreating ice and was impounded to form glacial lakes such as Lakes Agassiz, Regina and Saskatoon.

Streams and rivers, such as the South Saskatchewan River, draining into these lakes widened and slowed, thus decreasing the load capacity of the water for sediments. Consequently, large delta areas were formed consisting mainly of sand particles. The finer particles were carried further into the lakes giving origin to heavy clay deposits as are found in the Regina Plains area. The sand deposits have since been reworked by prevailing effective winds into parabolic dunes, the most common type found in semi-arid areas.

Parabolic dunes are usually partly covered with vegetation even while they are being formed (Hack 1941; Flint 1957; Odynsky 1958) and have a characteristic form, with the ridges convex downwind and the lee slope on the downwind side. The lee slope commonly has an angle of approximately 33 degrees (the natural angle of repose of sand), but the angle of the long windward slope is considerably less (5 degrees) (Cooper 1958). Dunes of this type often coalesce to form large sand sheets.

Deflation of finer particles from the windward slope of a dune or from a blowout bottom results in a residue of coarser material in these areas and a gradient of particle sizes, towards a finer texture, existing up the windward slope, over the dune crest and onto the lee slope. This differential blowing may have resulted in uneven distribution of particles on the dune topography, so that depressions adjacent to blowing areas and lee slopes received a greater amount of smaller particles, which has subsequently been important in soil formation and development of the vegetation.

Dune movement is usually along the axis of the most effective wind direction. In Saskatchewan, most of the dunes appear to have a north-west to south-east orientation. Movement rates were not measured and the literature revealed no information concerning movement rates in Saskatchewan dunes. Rates reported in other areas, however, vary from 5 to 22 feet per annum (Cowles 1911; Gates 1950; Ranwell 1958).

Climate

The regional climatic conditions in the study areas are related directly to Saskatchewan's location in the interior of the North American continent, the absence of modifying bodies of water, its mid-northern latitudinal location and the presence of the Rocky

Mountain Cordillera to the west (Coupland 1950). The most characteristic features of the climate are low precipitation and cool temperatures, factors of great importance in determining plant distributions. Precipitation is lowest in the extreme southwestern section of the province and gradually increases to the northeast, whereas temperatures are highest in the southwest and decrease to the north.

Table 1 illustrates the climatic conditions at two stations selected to represent the Dundurn and Great Sand Hills study areas. Annual precipitation in the two areas is about the same, but the mean annual and mean growing season (May-September) temperatures are less in the Dundurn area. The lower temperatures result in a slightly lower evaporation rate and a higher P/E ratio in the Dundurn area. The implications that climatic variations have with regard to the finer-textured soils (Mitchell *et al*. 1944) and the vegetation occurring on such soils (Coupland 1950, 1961) are well established. It remains, however, to be ascertained if similar effects are exhibited by vegetation occurring on sand dunes under these climatic regimes. Additional factors that may be important include distribution of rainfall and wind velocity, particularly the latter, through its effect on the physiography.

Vegetation Surrounding the Study Areas

The finer-textured soils surrounding the dune sand deposits support grassland vegetation that has been described by Coupland (1950, 1961) as a part of the Mixed Prairie. This grassland is dominated by *Stipa comata*, *S. spartea* var. *curtiseta*, *Agropyron* spp., *Koeleria cristata*, *Bouteloua gracilis* and *Carex* spp.

Table 1. A comparison of climatological conditions at two stations which approximate the conditions in the Dundurn (Saskatoon) and Great Sand Hills (Swift Current) study areas. (After Coupland 1960).

Station Soil zone	Swift Current Brown	Saskatoon Dark-Brown
Mean temperature (F)		
Annual	38	34
May-September	59	58
Annual precipitation (in.)		
1929-1958	13.51	13.46
Evaporation (in.)		
May-September	29.46	25.52
P/E ratio	0.48	0.54

Northward and northeastward, the Mixed Prairie is gradually replaced by the Fescue Prairie (*Festuca scabrella*) (Coupland and Brayshaw 1953), a grassland forming an important part of the aspen (*Populus tremuloides*) parkland. The aspen parkland is the transitional zone between the grasslands and the Boreal Forest (*Picea glauca*, *P. mariana*, *Larix laricina*, etc.) to the north.

The Mixed Prairie is bordered on the east by the True Prairie, on the west by the grasslands and forest of the Rocky Mountain foothills and on the south by the vast Great Plains area. The last region ranges from Saskatchewan to southern Texas and has been the study area for investigations too numerous to mention here.

METHODS AND PROCEDURES

Selection of Stands

Selection of sampling sites as representative of a certain plant community involves subjective judgment on the part of the selector, which introduces considerable bias into the sample. In order to study species distributional patterns formed in response to environmental gradients, it is important that selection of sampling sites be objective. The stands should be chosen on the basis of previously established criteria that exclude any reference to the specific composition of the vegetation. To facilitate objective sampling in this study, various physiographic categories were established in which stands were selected for vegetational and edaphic analysis.

In all, five physiographic categories were selected in the two study areas. Four of these were represented in the Dundurn area. They were: active complexes, stabilized blowouts, stabilized dunes and dune depressions. The criteria used to delimit the positions include: (1) Active complexes must have erosion or deposition taking place. (2) Stabilized blowouts, which were distinct saucer-shaped depressions aligned in the direction of the prevailing effective wind, must have evidence of recent erosion, but no erosion at present. (3) Stabilized dunes must show a characteristic dune form (windward and lee slopes) and have no evidence of recent erosion. (4) Dune depressions, which were usually located on stabilized dunes, must have no evidence of recent erosion. The last criterion was particularly important in differentiating between dune depressions and stabilized blowouts, which were also depressional but showed evidence of recent erosion.

Only three physiographic categories were selected in the Great Sand Hills. They were: active complexes, stabilized dunes and sand flats. The first two positions were the same as in the Dundurn area, whereas the sand flats, which were level stabilized areas between the dunes, represented a new physiographic type. It should be emphasized that selection of these positions was only to facilitate sampling of the vegetation, not to ascertain the geomorphological nature of the dunes. It is likely that they represent only a general view of the dune geology in the areas.

Within these positions, vegetational stands, meeting preestablished criteria of minimum size (100 square meters) and non-disturbance, were selected for compositional analysis. An attempt was made to include an equal number of stands in each physiographic position in the sampling, but this proved impossible because stands occurring on certain of the positions, particularly active complexes, were difficult to locate. In the Dundurn area, stable blowouts, stable dunes and dune depressions constitute the major portion of the topography, whereas active complexes are uncommon. The situation is different in the Great Sand Hills, where active areas are a more important aspect of the physiography.

An additional stand criterion was that the stands be homogeneous in composition. The field selection of a homogeneous unit is subject to considerable bias on the part of the selector. Field estimates of homogeneity, however, can be checked in the laboratory. The homogeneity of all stands sampled in this study was determined by utilizing the number of quadrats of occurrence of the two most frequent species in each stand. Dividing the number of occurrences by four gave an expected number of occurrences for the species in each of four sequential quadrat sub-samples in the total sample. The observed number of occurrences in each of the sub-samples was then used to obtain the deviation from the expected occurrence. A Chi-square test was applied and all but three stands were found to be homogeneous at the 5 % level. These three stands were not used in any of the subsequent interpretive analyses.

Field Vegetational Analyses

The field work was initiated in July of 1959 and continued through 1961. During this time, 63 stands were sampled by the point-centered quarter method (Cottam and Curtis 1956; Dix 1961) for herbaceous, shrub and tree composition. Within each stand sampled by this technique, 40 points were used. The placement of the pin was determined by pacing a preestablished distance along lines arranged to cover the entire stand. This method yielded information as to the relative density, relative frequency and absolute density (shoots per m^2) of the species. The relative density and relative frequency were summed to give a composite index termed importance value (IV), which gives a more informative measure of the success of a species than either of the component measurements.

Frequency determinations were also made, by use of 40 one-quarter m^2 quadrats, in each of the 63 stands and in an additional 38 stands, giving a total of 101 stands sampled in this manner. Density of rooted-shoots of forbs was also noted in some stands. The one-quarter m^2 quadrat resulted in frequency values greater than the 86% desired for the most common species as suggested by Curtis and McIntosh (1950), but an equal number of smaller quadrats, which achieved the 86% frequency figure, resulted in a decrease in the number of species encountered.

The decrease was not desirable, because these data were to be used in stand similarity tests, which become increasingly accurate when larger numbers of species are involved. It would have been necessary to observe more small quadrats per stand in order to encounter the same number of species as observed with the larger quadrats.

Line transects were established along compass lines in 12 stands to determine shrub canopy cover. The interception of the line by shrubs was recorded in inches and the percentage ground covered by the shrub canopy was calculated by dividing the total length of the transect into the intercepted distances and multiplying by 100. The transects varied in length from 100 to 150 feet.

Stands occurring on stabilized dunes and dune depressions were sampled by the ten-point frame (Clarke *et al*. 1942) to ascertain the percentage basal cover and composition. The same apparatus was used to ascertain the percentage ground cover in stands where *Juniperus horizontalis* was present. This was done by placing the point frame throughout the stand and recording the number of times a pin touched any portion of the *Juniperus* foliage. An estimate of the percentage cover was then calculated by dividing the number of hits by the total number of points observed and multiplying by 100.

Soil Analyses

Soil samples were taken at preselected depths in many stands in which the vegetation was analyzed. The sampling depths were selected independently rather than by horizons, because of the absence of profile development. The depths sampled were: 0-2", 2-4", 4-6", 6-12", 12-24", 24-36". The soil samples were air dried and passed through a 2 mm. sieve to remove roots and debris and to bring them to a uniform condition. All analyses were then performed on the sieved soil.

Dry soil color was determined by comparison with colors in the Munsell color chart 10YR. pH determinations were made on a saturated soil paste using a Beckman pH meter. Presence of $CaCO_3$ was determined by placing dilute hydrochloric acid on a sample and qualitatively rating the effervescence according to the following scale.

Scale	Effervescence
0	none
1	trace
2	slight
3	medium
4	strong

Estimates of organic matter (OM) in the samples were made by the loss on ignition technique. The samples were weighed, ignited at 420°C. for 8 hours and reweighed for loss of weight, which was considered the organic matter content. The percentage organic matter was then calculated on the basis of weight loss divided by original weight, multiplied by 100.

Water-retaining capacity (WRC) of the soil was determined by use of Hilgard cups. This characteristic is a useful, rapidly obtained measure of soil moisture status, reflecting organic and textural qualities of the soil.

Soil texture was determined by the Bouyucous (1951) hydrometer method, yielding data on percentage sand, silt, and clay in the samples. It has been shown that, although not as accurate as the pipette analysis, the hydrometer method can be used for rapid analysis of soils low in organic matter (Toogood and Peters 1953).

Preliminary work was done in the Dundurn study area to determine the soil moisture content at various depths on the selected physiographic positions. Two separate stations were established on each of the four positions from which soil samples were taken throughout the growing season of 1961 at the same depths as for the soil analyses. The samples were placed in friction lid cans, taped to prevent moisture loss, transported to the laboratory, weighed, dried at 105°C. for 48 hours and reweighed. The percentage moisture present was calculated from the loss of weight on drying. All calculations were on the basis of oven-dry soils.

Plant specimens were collected in the study areas and placed in the W. P. Fraser Herbarium (SASK.). Nomenclature is according to Moss (1959).

RESULTS

Nature of the Analytical Technique

The study of native vegetation can be divided into two main approaches, qualitative and quantitative. Early ecological work tended to be qualitative, probably because of its out-growth from natural history. As ecology has developed, quantification of its methods has progressed greatly, but even the most enthusiastic realize that quantitative ecology has just begun. Contemporary plant ecology is best described as a complexity of both procedures.

Qualitative or descriptive plant ecology has its merits, particularly where broad areas are to be studied over relatively short periods of time. Greig-Smith (1957) and others, however, advocate more exacting methods in plant ecology and feel that great advances can be expected from the quantitative techniques now being developed.

Clements (1916) had a profound effect upon the thinking of many contemporary plant ecologists in proposing the theory that plant communities are discrete units, repeated in space and time. This concept had a particular influence on the development of ecological research methods, in that the need for more exact and rapid methods of measuring vegetation was curtailed by the idea that very few stands of vegetation need be studied in order to describe the composition. Some workers, who followed Clements' ideas on the nature and structure of vegetation, did realize, nevertheless, that vegetation could be better described when extensive sampling was done. Coupland (1950), for example, studied approximately 150 sites in describing the prairies of Saskatchewan and Alberta.

In opposition to the concept of vegetation as discrete units, there arose the continuum theory (Curtis and McIntosh 1951) that postulated that vegetation is not composed of divisions inherent in the vegetation, but of a continuous array of species populations from one end of some environmental gradient to the other. This theory is based on the individualistic concept of Gleason (1926) that proposed that only where tolerances of species to environmental factors overlap will there be a unit that could be denoted as a distinct community, and if it were, the distinction would be a subjective one made by the observer and not an inherent part of the vegetation (Goodall 1961). These concepts of population continua have resulted in many methods for describing the vegetation in uni- or multi-dimensional systems. The general term applied to such schemes is "ordination" (Goodall 1953). The most elaborate ordination technique is based on factor analysis, in which correlation coefficients between species associations are used (Goodall 1953, 1954a, 1954b, 1961; de Vries 1954). Such techniques, however, require use of computers and thus a less exact but more economical (time and money) technique has been proposed by Curtis and his associates, the leading advocates of ordination methods in North America.

Curtis and McIntosh (1951) studied upland hardwood forests in southwestern Wisconsin, which met certain preestablished criteria, to determine composition and structure. They objectively assigned climax adaptation numbers to the principal species, which were then used to weight importance values (relative frequency + relative density + relative dominance = importance value) for each of the species in a given stand. It was thus possible to assign an index number, ranging theoretically from 300 to 3,000, to each stand. When this was done, it was found that no distinct groups of stands occurred, but that a continuum of stands was exhibited. Species distributions plotted against the stand continuum formed bell-shaped curves, the result of environmental complexes affecting the plants. Curtis (1955) using presence values ordinated 157 prairie stands and found that these stands also represented a vegetational continuum.

Bray and Curtis (1957) studied upland forest stands of southern Wisconsin using a geometrical method of stand ordination. In this study, more than one ordination axis was computed, since it was observed that the first axis placed stands close together that in reality were quite different. A second and finally a third axis was established in order to separate such groupings. Relation of the various axes with environment showed that each was correlated either with soil factors or cultural practices during early settlement.

Dix (1958), studying slope-plant relations in North Dakota, reported species distributions in response to a moisture gradient. In this study, the ordination was accomplished by use of similarity coefficients (Sorensen 1948). A similar study was done by Dix and Butler (1960), in a prairie in Wisconsin, also using similarity coefficients to arrange sample plots within the prairie in a linear order. Densities of species plotted against the ordination exhibited approximately normal distributions in most cases. The causal agent in the distributions was suspected to be soil depth, which influenced local soil moisture.

In a somewhat more elaborate ordination process, Beals (1960) studied bird communities in the Apostle Islands of Wisconsin. This method also utilized similarity coefficients, but interstand separation was accomplished by a modification of the method described by Bray and Curtis (1957). This same method was used by Beals and Cottam (1960) in describing forest vegetation in the area.

Maycock and Curtis (1960) used ordination methods in describing boreal conifer - hardwood forests of the Great Lakes region. They computed stand positions along three axes and found that species behaviors along the axes resembled a series of integrading spherical distributions, with no species exhibiting identical curves. Rice and Penfound (1959) analyzed upland forest vegetation of Oklahoma by plotting species distribution along moisture and geographical gradients. The results indicated a continuity of vegetation as found by Curtis and his associates.

In a more practical aspect, Dix (1959) used grazing susceptibility numbers for various species to weight relative density values in ordinating stands. Density of individual species was then plotted against the ordination to illustrate the effects of grazing pressure.

It is not the purpose of this study to question the reality of vegetational units. Nevertheless, the author feels that until sufficient data are obtained establishing the distinctness of plant communities, it is better to describe the vegetation on a continuum basis. Recognition of a vegetational continuum does not exclude the existence of separate vegetational communities (Greig-Smith 1957; Goodall 1961), since species with similar tolerances could be considered as communities within the vegetational continua, but the deliniation would be a subjective one. The abstract classification of vegetation into communities implies the concrete nature of these in the field. The converse is not necessarily true; communities might be sharply defined in the field, but form a continuum that can not be classified except by arbitrary divisions.

Treatment and Interpretation of Data

Physiographic Gradient. —— One means of gradient analysis in phytosociological research involves presentation of vegetational composition with reference to previously established categories; *i.e.*, soil texture, altitude or physiography. Whittaker (1960) used such an approach in presenting data with reference to moisture and altitude gradients. Using this approach, once stands are sampled within the categories, and these data averaged for each category, an indication of the composition within and changes along the various gradients represented by the categories will be available. The distributions can then be correlated with environmental factors present in the categories.

The first portion of this section will utilize the above approach in analyzing the vegetation in each of the two study areas. The categories used in sampling the vegetation were physiographic and have been described previously (see METHODS AND PROCEDURES).

Importance values, absolute densities, frequencies and quadrat presence values (the number of times a species is present in at least one quadrat in a stand, divided by the total number of stands in that category) were averaged for stands within each physiographic position.

Dundurn

Active Complexes. —— Three taxa attained importance on blowouts and dunes in the Dundurn area; Agropyron spp., Psoralea lanceolata and Artemisia campestris (Table 2) (Fig. 2). The total density was low, only 22.6 plants per m^2. The first and second ranked species are rhizomatous, a morphological characteristic often reported for pioneer sand dune species (Ramaley 1939; Ranwell 1960). Corispermum orientale, an annual, was the fourth ranked species. Although only these species were important, many other plants encountered on dunes and blowouts have often been reported growing in similar habitats in other dune areas (Pool 1914; Bird 1927; Ramaley 1939). It is interesting that, except for Agropyron spp., the important plants of active complexes are forbs. The few grasses present have low importance values.

Stabilized Blowouts. —— Stabilization of actively blowing areas occurs slowly. Stable forms of once active dunes can be recognized by the characteristic chapes they possess, such as lee and windward slopes. Stabilized blowouts usually appear as saucer-shaped depressions oriented in the direction of the prevailing effective wind (Odynsky 1958).

Three conditions may result in cessation of sand erosion from blowouts. The blowout may deepen until the water table is near the sand surface resulting in a decrease in erosion, the blowout may become so deep that the effective wind erosional action is reduced to a degree that no longer is it able to transport sand particles (Pool 1914) and erosion may cease if an unerodable surface is reached (Ranwell 1958).

Table 2. Importance value (IV) and absolute density (AD) for the major species in the various physiographic habitats in the Dundurn area.

Physiographic position	Active complexes		Stabilized blowouts		Stabilized dunes		Dune depressions	
	IV	AD	IV	AD	IV	AD	IV	AD
Species								
Agropyron spp.	56.0	7.1	35.0	9.5	9.0	16.6	4.0	12.7
Artemisia campestris	39.0	4.6	2.8	0.4	0.3	0.3	0.5	2.0
Artemisia frigida	-	-	3.0	0.7	11.0	15.2	1.0	2.0
Artemisia ludoviciana	-	-	-	-	-	-	11.0	30.3
Bouteloua gracilis	-	-	-	-	7.0	13.4	3.0	8.8
Calamovilfa longifolia	6.0	0.4	15.0	3.6	11.0	18.7	3.0	8.0
Campanula rotundifolia	-	-	0.8	0.2	0.2	0.3	-	-
Carex eleocharis	-	-	3.0	1.4	44.0	75.8	4.0	15.6
Carex heliophila	-	-	74.0	22.7	18.0	37.5	152.0	819.8
Chrysopsis villosa	2.5	0.3	0.9	0.2	2.0	2.8	-	-
Corispermum orientale	23.0	2.4	-	-	-	-	-	-
Elymus canadensis	1.1	0.1	-	-	-	-	-	-
Equisetum hymale	-	-	2.9	0.6	-	-	-	-

Table 2 - Continued

Physiographic position	Active complexes		Stabilized blowouts		Stabilized dunes		Dune depressions	
	IV	AD	IV	AD	IV	AD	IV	AD
Festuca ovina	-	-	8.0	1.4	0.7	1.1	-	-
Helianthus petiolaris	3.0	0.4	-	-	-	-	-	-
Koeleria cristata	5.0	0.4	9.0	2.2	17.0	27.5	7.0	20.5
Lygodesmia juncea	10.0	1.0	-	-	-	-	-	-
Oryzopsis hymenoides	5.0	0.2	-	-	-	-	-	-
Petalostemon purpurem	-	-	3.0	0.7	0.3	0.3	-	-
Phlox hoodii	-	-	-	-	4.0	6.4	0.4	1.0
Psoralea lanceolata	44.0	5.2	10.0	2.2	0.9	1.1	-	-
Solidago missouriensis	-	-	9.0	2.2	-	-	1.0	2.0
Sporobolus cryptandrus	4.0	0.3	0.8	0.2	44.0	6.4	-	-
Stipa comata	-	-	6.0	1.4	65.0	124.6	11.0	38.1
Other species	1.4	0.2	16.8	3.5	5.6	5.0	2.1	8.9
Total	200.0	22.6	200.0	53.1	200.0	353.0	200.0	969.7

Fig. 2. Actively blowing sand complex in the Dundurn area. Species present are Psoralea lanceolata and Rumex venosus.

It is possible that in the Dundurn area two of these factors are operating, since deep blowouts and hard floors in blowouts have been observed.

The vegetational composition of stabilized blowouts can be seen from Table 2. These data represent average IV, for the first ten ranked herbaceous species on each physiographic position. An additional species acting as a stabilatory agent on blowouts is Juniperus horizontalis (Fig. 3). This prostrate shrub has a mean ground cover of 78% and a range of 59.7% to 92.5% in the 12 stabilized blowouts sampled. Van Denack (1961) reported that this species, along with Arctostaphylos uva-ursi, established growth centers on stable edges of blowouts, extended creeping branches (Fig. 4) into the blowout and founded a disjunct growth patch. Cowles (1899) also reported that windward dune slopes near Lake Michigan were clothed by Juniperus horizontalis, J. communis and Arctostaphylos uva-ursi. The presence of these species in the severe blowout and windward slope habitats was attributed to their sclerophyllous morphology which prevented excessive transpiration.

Even though stabilized blowouts are often covered by dense mats of these evergreen species, there are still many herbaceous plants present. The most important of these is Carex heliophila, a small prairie sedge, which Coupland (1950) reported as occurring in favored locations. Agropyron spp. is also an important herbaceous constituent of the vegetation. The third ranked graminoid in this habitat is Calamovilfa longifolia, a common sand dune inhabitant in North America (Pool 1914; Ramaley 1939; Tolstead 1942; Van Denack 1961). The rhizomatous habit of this plant makes it an

Fig. 3. Stabilized blowout in the Dundurn area. The prostrate shrub is Juniperus horizontalis.

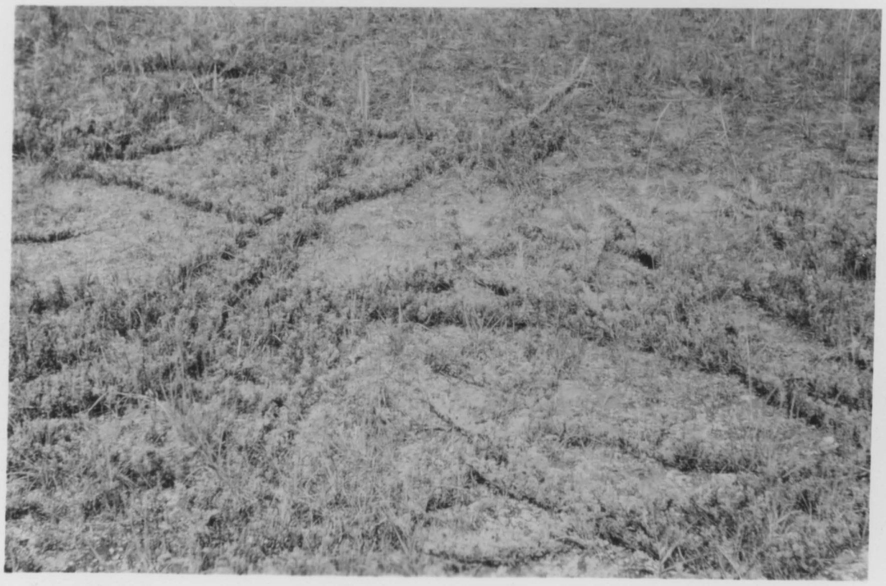

Fig. 4. Creeping branches of Juniperus horizontalis invading a blowout in the Dundurn area.

excellent sand binder (Fig. 5). Occurring in both erosional and depositional areas (Waterman 1923), it is apparently tolerant due to its mode of vegetative reproduction by short rhizomes, initially pointed downward at a slight angle in late summer and later extending upwards to give rise to new shoots the next year regardless of whether limited erosion or deposition has occurred (Olson 1958; Van Denack 1961).

Total absolute density in stabilized blowouts is greater than in active blowout-dune complexes: 53 to 23 plants per m^2 for the two positions, respectively. Psoralea lanceolata, the second ranked species on active areas, is not as important in stabilized blowouts, while Stipa comata and Koeleria cristata, common grasses in Saskatchewan prairies (Coupland 1960), are more important. Six of the ten important species on the active complexes are absent from the stabilized blowouts, which indicates the narrow tolerance of these species to changes in environment.

The variation in Juniperus horizontalis ground cover on stable blowouts is accompanied by an inverse variation in forb density ($r = -.88$). The high forb density occurring under the low cover was due primarily to local aggregations of species, such as Cerastium arvense.

Stabilized Dunes.—— Dune stabilization results in a different vegetational structure than that of blowout stabilization and as on preceeding positions, there is an increase in absolute density (Table 2). Stipa comata, Carex eleocharis and Sporobolus cryptandrus are the major components of the vegetation (Fig. 6). The second species has been reported as the most abundant member of the genus in the Canadian Mixed Prairie on soils of finer texture (Coupland 1950).

Fig. 5. Sand hummocks formed by _Calamovilfa longifolia_ because of its extensive root-rhizome system, which reduces erosion.

Fig. 6. Stabilized dune in the Dundurn area. The dominant grass is Stipa comata.

Carex heliophila, an important plant on stable blowouts, is of considerably less importance on stable dunes. Conversely, *Koeleria cristata* has an importance value of only 5 on active complexes and 9 on stable blowouts, while it is 17 on stabilized dunes.

Artemisia frigida is the most important forb on stabilized dunes in the Dundurn area. Coupland (1950) reported the rooted shoot density per m^2 of this species in grasslands on finer-textured soils to be from 5 to 10, but in the present investigation it was found that on stabilized dunes near Dundurn, the density reached 15 shoots per m^2. The use of different methods in determining density may explain the difference.

Stabilization of dunes results in the presence of another grass becoming evident. *Bouteloua gracilis*, the only important short grass in Canada, had an importance value of 7 on stable dunes. This species is shallowly rooted, but has extensive lateral root development (Johnson 1960). Field observations indicated that *Bouteloua* may be more prevalent on exposed south-west facing slopes, but further study is needed to determine if this is the situation.

Additional analysis of 17 stabilized dune stands with the point-transect also revealed that *Stipa comata* was the dominant plant, exclusive of *Selaginella densa* (Table 3). However, the basal cover of the latter species was 23.8%, while for *Stipa comata* it was only 5.9%. The lesser importance of *Carex eleocharis*, *Artemisia frigida*, *Calamovilfa longifolia*, *Carex heliophila* and *Koeleria cristata* is evident from Table 3.

Dune Depressions. —— The fourth physiographic position in the Dundurn area is present in the form of saucer-shaped depressions on

Table 3. Percentage basal cover and composition in seventeen stabilized dune stands in the Dundurn area.

Species	Percentage basal cover	Percentage composition
Selaginella densa	23.8	57.2
Stipa comata	5.9	14.2
Carex eleocharis	2.1	5.6
Artemisia frigida	1.9	4.6
Koeleria cristata	1.8	4.3
Calamovilfa longifolia	1.7	4.1
Carex heliophila	1.1	2.6
Bouteloua gracilis	0.6	1.4
Phlox hoodii	0.3	0.7
Chrysopsis villosa	0.3	0.7
Agropyron spp.	0.2	0.5
Other species	1.7	4.1
Total	41.7	100.0

stabilized dunes (Fig. 7). The exact origin of the depressions is not known, but such physiographic phenomena have been reported in the literature. Ranwell (1958), working in Wales, termed similar depressions dune "slacks" and attributed their origin to blowout erosion down to the water table where erosion ceased. The same explanation for their presence in Saskatchewan dunes is not completely justified, due to a greater depth of the water table, estimated at 10 to 12 feet, and lack of evidence that a water table at this depth could sufficiently affect the resistance of the sand to erosion. An alternative explanation is that the depressions were formed in the initial deposition of the sand and have since resisted erosion because of the type of vegetation which occurs there.

Inspection of the composition of these depressions (Table 2) and a knowledge that many of these species are indicative of more abundant moisture suggests that the depressions are mesic. The highest importance value is 152 (Carex heliophila) and the absolute density is the greatest measured on any position, 969.7 shoots per m^2. Most of this denseness (84%) is due to Carex heliophila.

The overwhelming dominance of Carex heliophila in depressions is also illustrated by Table 4. The percentage composition is 42.31 and the percentage basal cover is 11.50. The only other important plant is Selaginella densa, a species not recorded in sampling with the point-center quarter method, because its high density would have made it necessary to observe many additional points in order to sample other less dense species adequately.

Extensive shrub patches occur within or on the edge of depressional areas. Table 5 illustrates the composition of such stands

Fig. 7. A dune depression in the Dundurn area. Note the dark green color in the foreground (depression) as compared to the lighter color of the stabilized dune in the background.

Table 4. Percentage basal cover and composition in six dune depression stands in the Dundurn area.

Species	Percentage basal cover	Percentage composition
Selaginella densa	11.7	42.9
Carex heliophila	11.5	42.3
Calamovilfa longifolia	0.8	2.8
Stipa comata	0.8	2.8
Agropyron spp.	0.6	2.4
Stipa spartea var. *curtiseta*	0.5	2.0
Bouteloua gracilis	0.5	1.8
Geum triflorum	0.3	1.0
Koeleria cristata	0.1	0.5
Artemisia gnaphalodes	0.1	0.5
Artemisia frigida	0.1	0.5
Artemisia campestris	0.1	0.2
Helictotrichon hookerii	0.1	0.2
Total	27.2	100.0

Table 5. Percentage canopy cover, as determined by 18 line transects in 12 shrub stands occurring on stabilized dune and dune depression physiographic positions in the Dundurn area.

Species	Percentage canopy cover
Symphoricarpos occidentalis	12.15
Prunus virginiana	3.37
Elaeagnus commutata	2.61
Rosa woodsii	1.17
Shepherdia argentea	0.59
Rhus radicans var. *rydbergii*	0.01
Total	19.90

on the basis of percentage canopy cover. Symphoricarpos occidentalis, Prunus virginiana and Elaeagnus commutata are commonly associated with coarse-textured soils in Saskatchewan (Coupland 1950). An inverse relationship ($r = -.79$) occurred between forb density and percentage canopy cover in these shrub patches. Although there was a decrease in forb density with increased canopy cover, there was an increase in total density, due to the larger importance assumed by Carex heliophila under dense canopies.

Table 6 demonstrates the variations in frequency and quadrat-presence (Q-P) between the four physiographic positions in the Dundurn area. Psoralea lanceolata, for example, has a frequency of 66% and a Q-P of 100% on active complexes, indicating that this species occurred in at least one quadrat in every stand analyzed on active complexes and was frequent in those stands in which it occurred. In stands located on stabilized blowouts, the percentage frequency is less as is the quadrat-presence. Psoralea is usually present in stabilized blowout stands, but is not frequent in the vegetational composition. The reverse situation is true of stabilized dunes. On such sites, Psoralea is present in only 66% of stands sampled, but attains a frequency of 44% in the stands of occurrence. Dune depressions represent the habitat in which Psoralea lanceolata is lowest in frequency. The plant is present, however, in 66% of the stands sampled in depressions, which indicates its wide ecological amplitude to factors present in the entire dune environment.

Similar variations in frequency and quadrat-presence along the physiographic gradient are shown by many species in the Dundurn area. Some of the plants are most frequent in stands on active complexes;

Table 6. Percentage frequency (F) and quadrat-presence (Q-P) for the twenty-five most important species in stands in each of the four selected physiographic positions in the Dundurn area.

Physiographic position	Active complexes		Stabilized blowouts		Stabilized dunes		Dune depressions	
	% F	% Q-P	% F	% Q-P	% F	% Q-P	% F	% Q-P
Species								
Agropyron spp.	53	80	56	100	40	57	51	100
Ambrosia artemisiafolia	23	10	-	-	-	-	-	-
Amelanchier alnifolia	-	-	-	-	88	4	95	11
Androsace septentrionalis	-	-	-	-	-	-	3	22
Arabis holboellii	5	10	6	33	15	52	10	11
Arctostaphylos uva-ursi	-	-	51	16	18	4	-	-
Artemisia campestris	43	30	6	41	14	61	10	22
Artemisia frigida	-	-	19	91	64	100	13	77
Artemisia ludoviciana	-	-	6	16	16	9	53	100
Bouteloua gracilis	-	-	5	25	28	52	16	77
Calamagrostis montanensis	3	10	8	33	6	28	17	11
Calamovilfa longifolia	37	40	27	91	42	57	37	66
Campanula rotundifolia	-	-	8	50	5	23	11	44
Carex eleocharis	5	10	53	8	77	61	5	11
Carex filifolia	-	-	8	25	25	23	5	11
Carex heliophila	3	10	80	100	79	47	98	100
Cerastium arvense	-	-	24	16	29	19	12	55
Chrysopsis villosa	23	20	8	75	34	80	16	33
Commandra pallida	3	10	19	41	3	4	8	11
Corispermum orientale	10	70	-	-	-	-	-	-
Elaeagnus commutata	12	50	5	25	-	-	-	-
Elymus canadensis	4	30	-	-	4	9	-	-
Equisetum hyemale	3	10	63	8	38	9	-	-
Erigeron caespitosis	-	-	43	8	10	19	3	11
Festuca ovina var. *saximontana*	-	-	31	16	10	4	3	11

Table 6 - Continued

Physiographic position	Active complexes		Stabilized blowouts		Stabilized dunes		Dune depressions	
	% F	% Q-P	% F	% Q-P	% F	% Q-P	% F	% Q-P
Species								
Gaura coccinea	-	-	-	-	15	14	15	11
Geum triflorum	-	-	5	8	5	4	10	66
Helianthus petiolaris	24	80	-	-	-	-	-	-
Helictotrichon hookeri	-	-	7	33	18	19	3	11
Juniperus horizontalis	-	-	99	100	36	9	8	11
Koeleria cristata	48	10	32	75	50	95	13	66
Lepidium densiflorum	5	10	-	-	9	9	-	-
Linum rigidum	5	20	3	8	-	-	-	-
Lygodesmia juncea	33	60	8	8	12	42	5	22
Oenothera spp.	-	-	-	-	10	4	45	11
Oryzopsis hymenoides	12	80	-	-	-	-	-	-
Oxytropis macounii	-	-	11	41	-	-	-	-
Pentstemon nitidus	5	10	3	8	3	4	-	-
Petalostemon purpureus	-	-	9	83	15	33	-	-
Phlox hoodii	-	-	22	25	25	61	13	11
Prunus virginiana	-	-	8	8	84	14	-	-
Psoralea lanceolata	66	100	22	91	46	66	28	66
Rosa woodsii	15	10	8	33	23	33	14	66
Salsola kali	13	30	-	-	-	-	3	11
Selaginella densa	20	10	87	83	65	90	72	33
Shepherdia argentea	-	-	-	-	-	-	45	11
Smilicina stellata	-	-	5	8	18	28	-	-
Solidago missouriensis	5	10	26	100	19	33	25	88
Sporobolus cryptandrus	12	60	-	-	28	28	-	-
Stipa comata	6	30	24	75	82	95	34	66
Stipa spartea var. curtiseta	-	-	-	-	5	4	56	33
Stipa viridula	-	-	-	-	3	4	-	-
Symphoricarpos occidentalis	-	-	45	8	59	19	54	66

e.g., *Psoralea lanceolata*, *Agropyron* spp., *Helianthus petiolaris*, *Corisperum orientale*, *Oryzopsis hymenoides*, *Lygodesmia juncea* and *Sporobolus cryptandrus* (Table 6). Along with these species, there occur consistently a number of species that are not as important in terms of percentage frequency. Some of these species are, however, important constituents of the vegetation in stands on other physiographic positions. *Juniperus horizontalis*, for example, did not occur in any of the active complex stands, but was the most important plant on stabilized blowouts. Similarly, *Carex heliophila*, *Solidago missouriensis*, *Arctostaphylos uva-ursi* and many other species were of greater significance in the vegetation in stabilized blowouts than of that in active areas.

The same situation is present on the other two physiographic sites, stabilized dunes and dune depressions. In general, the distributional patterns are similar to those exhibited in Table 2, in that the values approximate normal distributions. Many species, however, have abrupt changes and evidences of bimodal distributions (*Carex heliophila*, *Agropyron* spp., *Sporobolus cryptandrus* and *Solidago missouriensis*) (Table 6).

Sceptre

The physiography of the Great Sand Hills, south of Sceptre, Lemsford and Portreeve, differs from that encountered near Dundurn. Four physiographic positions were described in the latter area, whereas only three positions were differentiated in the former. These include: active blowout-dune complexes, stabilized dunes, and sand flats. The sand flats represent a different position, while stabilized blowouts and dune depressional areas were not as evident in the topography (Fig. 8).

Active Complexes. —— The vegetation occurring on actively blowing areas is similar to that in the Dundurn area (Table 7). However, rhizomatous (Fig. 9) *Psoralea lanceolata*, a plant characteristic of open dunes (Tolstead 1942), is the most important plant. *Agropyron* spp. was observed growing on open dunes in the Great Sand Hills, but was not encountered in the point-centered quarter sampling, which may be due to the relatively greater abundance of *Psoralea lanceolata*. *Rumex venosus* is, on the basis of the measured stands, present to a greater extent in the Great Sand Hills than in Dundurn dunes. It was, nevertheless, found in small localized areas on dunes in the latter area. Most plants on active complexes are common to both regions.

Active complex sampling in the Great Sand Hills may have included stands with a greater degree of stability than those sampled in the Dundurn area, which is evidenced in the greater total density. The more stable conditions resulted in greater importance values for two grasses, *Elymus canadensis* and *Calamovilfa longifolia* (Table 7). Of course, this physiographic position is subject to such violent fluctuations in density that these differences may not be significant.

Stabilized Dunes. —— Stabilization of dunes is initiated either in the blowout bottom or at the foot of windward and lee slopes. It was observed that active complexes gradually merged into stable dune grassland wherever erosion had been slowed sufficiently to allow growth by less adapted plants. Table 8 illustrates the change from a simple (four species) structure on dunes to a more complex

Fig. 8. General view of the physiography in the study area south of Sceptre.

Table 7. Importance value (IV) and absolute density (AD) for the major species in the various physiographic habitats in the Sceptre area.

Physiographic position	Active complexes		Stabilized dunes		Sand flats	
	IV	AD	IV	AD	IV	AD
Species						
Agropyron spp.	-	-	3.0	2.0	20.1	5.9
Artemisia campestris	13.0	3.0	32.0	24.0	2.9	0.6
Artemisia frigida	-	-	5.0	3.4	1.8	0.3
Calamovilfa longifolia	20.0	4.3	32.0	27.7	1.1	0.3
Campanula rotundifolia	-	-	0.2	0.2	4.0	0.7
Carex eleocharis	-	-	0.2	0.2	-	-
Carex heliophila	-	-	0.7	0.5	88.0	24.6
Chrysopsis villosa	8.0	1.2	1.3	0.8	2.0	0.3
Corispermum orientale	13.0	2.4	-	-	-	-
Elymus canadensis	17.0	3.2	0.4	0.3	2.9	0.4
Equisetum hymale	-	-	0.3	0.2	5.0	1.1
Festuca ovina	-	-	3.0	2.1	21.0	4.9
Helianthus petiolaris	10.0	1.6	-	-	-	-
Juncus balticus	-	-	-	-	9.0	2.1
Koeleria cristata	1.0	0.2	26.0	20.4	12.0	2.5
Lygodesmia juncea	10.0	1.9	0.2	0.2	-	-
Oryzopsis hymenoides	10.0	1.6	0.4	0.4	-	-
Psoralea lanceolata	75.0	16.3	13.0	9.5	0.3	0.1
Rumex venosus	8.0	1.1	-	-	-	-
Solidago missouriensis	-	-	2.0	1.1	10.0	2.0
Sporobolus cryptandrus	5.5	1.0	12.0	10.9	-	-
Stipa comata	1.0	0.1	65.0	56.6	9.0	1.7
Other species	8.5	1.4	3.3	2.1	10.9	2.3
Total	200.0	39.3	200.0	162.6	200.0	49.8

Fig. 9. Exposure of rhizomes of Psoralea lanceolata due to erosion on the windward slope of an active dune in the Sceptre area.

Table 8. Quadrat transect from base of windward slope onto stabilized dune in the Sceptre area. Frequency data from $\frac{1}{4}$ m^2 quadrats is calculated for 1 - 20, 21 - 40 and 41 - 60 quadrat segment.

Number of quadrats from dune base	Frequency		
	1 - 20 quadrats	21 - 40 quadrats	41 - 60 quadrats
Species			
Psoralea lanceolata	55	100	100
Oryzopsis hymenoides	15	20	10
Helianthus petiolaris	10	15	-
Elymus canadensis	10	20	10
Chrysopsis villosa	-	32	30
Artemisia campestris	-	55	90
Linum rigidum	-	5	10
Sporobolus cryptandrus	-	10	30
Agropyron spp.	-	5	5
Stipa comata	-	-	50
Koeleria cristata	-	-	70
Solidago missouriensis	-	-	5
Arabis holboellii	-	-	10

(twelve species) structure 15 meters away. Psoralea lanceolata increased with movement away from the active area, but its relatively low frequency in the first 20 quadrats was due to the extensive bare sand and consequent low frequency of all species present. Koeleria cristata and Stipa comata attained high frequencies in quadrats 40 to 60, both plants are indicative of stable dune conditions. There was no decrease in pioneer plants, but this was probably due to insufficient extension of the transect into the stabilized dune. There was a marked decrease in the amount of bare sand from the first to the sixtieth quadrat.

Stabilized dunes support vegetation similar to that on the stabilized dunes in the Dundurn area (Table 7) (Fig. 10). Nevertheless, there are some differences, the most noticeable of which is the low value of Carex eleocharis. Sporobolus cryptandrus is more important on stable dunes near Sceptre which may reflect relatively unstable conditions of the dunes in the area. This plant has been reported as an indicator of pioneer stages of dune stabilization in many studies in the Great Plains (Pool 1914; Campbell 1929; Ramaley 1939; Tolstead 1942; and Coupland 1950). Table 9 indicates the percentage basal cover and composition for stabilized dunes as determined by the point transect method. The rank in importance for the species as determined by the two methods (point-centered quarter and point-transect) is similar. Percentage basal cover was low, although comparable with basal cover figures reported for grasslands on finer-textured soils in Saskatchewan by Coupland (1960). The total absolute density is greater on stabilized dunes than on active complexes. Stipa comata contributed 34.7% and Calamovilfa longifolia 17.0% of the

Fig. 10. Stabilized dune in the Sceptre area. The large shrub is Prunus virginiana.

Table 9. Percentage basal cover and composition in six stabilized dune stands in the Sceptre area.

Species	Percentage basal cover	Percentage composition
Stipa comata	7.1	56.2
Artemisia campestris	1.7	14.3
Calamovilfa longifolia	0.6	10.6
Koeleria cristata	1.1	9.9
Psoralea lanceolata	0.9	7.3
Artemisia frigida	0.2	1.2
Arabis holboellii	0.1	0.3
Chrysopsis villosa	0.1	0.2
Total	11.8	100.0

density on the stabilized dunes. This is similar to the change from primarily forbs to grasses that occurred with stabilization in the Dundurn area.

Stable dunes in the Great Sand Hills often support a shrub overstory (Fig. 11), in which the most common species is Artemisia cana (Table 10). Total shrub density is low (only 2.48 shoots per m^2), but because of their size they are conspicuous. Artemisia cana was not recorded in the Dundurn area, which is apparently beyond its geographical range.

Sand Flats. —— The third physiographic type described in the Great Sand Hills is in the form of large sand flats (Fig. 12). These appear to be base level areas (possibly a fine-textured lacustrine deposit) upon which the dunes are superimposed. The direction of dune movement across the flats as observed from air photos appears to be from north-west to south-east.

The most conspicuous plant on the flats is Juniperus horizontalis with a mean ground cover of 84%. This is somewhat higher than the Juniper cover in the stable blowouts at Dundurn. On some sand flats Juniperus was absent, but most such areas had been grazed extensively, thus making sampling impossible since non-disturbance was a stand criterion. In sand flats which had not been grazed heavily, Juniperus horizontalis is usually present. Whether a relationship exists between presence of this species and grazing is not known. Dirschl (1960) did find that Juniperus horizontalis is a major constituent of antelope diets in sandhills during the winter. Some grazed flats appeared to be saline and supported a heavy growth of Hordeum jubatum, Distichlis stricta and occasionally Triglochin maritima. Some Andropogon

Fig. 11. Artemisia cana on a stabilized dune in the Sceptre area.

Table 10. Importance value (IV) and absolute density (AD) for species of shrubs in five stabilized dune stands in the Sceptre area.

Species	IV	AD
Artemisia cana	146	1.88
Rosa woodsii	21	0.26
Symphoricarpos occidentalis	15	0.17
Prunus virginiana	10	0.09
Elaeagnus commutata	4	0.04
Rhus trilobata	4	0.04
Total	200	2.48

Fig. 12. Lee slope of a large sand dune in the Sceptre area. The dune is moving in an easterly direction across the sand flat.

scoparius was observed, but never in great abundance.

Herbaceous vegetation on sand flats, within the Juniperus mat, has Carex heliophila as the most important plant (Table 7), while the second ranked species is Festuca ovina var. saximontana. Many other species in this habitat are usually associated with high moisture conditions: Solidago missouriensis, Juncus balticus, Campanula rotundifolia and Equisetum hymale. Van Denack (1961) recorded many of the same genera and a few of the same species in similar habitats in the Lake Michigan area of Wisconsin as did Pound and Clements (1900) in Nebraska.

Total herb density is higher on this position than for actively blowing areas, but only one-third that on stabilized dunes (Table 7). It is interesting to note the similarity between total herb density in Dundurn stabilized blowouts (53.1) and that in sand flats in the Great Sand Hills (49.8). Whether the mean Juniperus cover of 84% in the latter area as compared to 79% in the former, is the factor causing the lower forb density in the sand flats is not known.

Shrubs are common in the sand flat habitat (Table 11). Elaeagnus commutata, Symphoricarpos occidentalis and Rosa woodsii were the first three ranked species. Total density is higher than on Sceptre stabilized dunes (8.7 and 2.5, respectively). The shrubs may occur in two distinct or integrading phases; clumped in slight depressions or widely scattered with no apparent pattern. Low ridges on the sand flats were observed to have fewer shrubs than on the sand flat proper which may be due to increase in elevation above the flat and a consequent change in the environment affecting shrub distribution. Shrubs were observed extending their range from the sand flats onto

Table 11. Importance value (IV) and absolute density (AD) for species of shrubs in four sand flat stands in the Sceptre area.

Species	IV	AD
Elaeagnus commutata	87	3.90
Symphoricarpos occidentalis	61	2.80
Rosa woodsii	40	1.50
Prunus virginiana	6	0.30
Salix bebbiana	4	0.10
Shepherdia argentea	1	0.05
Artemisia cana	1	0.05
Total	200	8.70

the dune base, but decreased in density with increased height above the level of the sand flat.

Populus tremuloides groves are common in the Great Sand Hills in depressions, which is analogous to Salix-Populus stands found in sand by Ramaley (1939) in Colorado. These are often even-aged pure stands, but may be of mixed age groups and contain Populus balsamifera (Maini 1960). No extensive sampling was done on groves in the Dundurn or Great Sand Hills areas for two reasons: firstly, Maini (1960) studied the nature and significance of groves in coarse-textured soils in both the dark-brown and brown soil zones and secondly, it was difficult to locate stands which were undisturbed. In areas where cattle were present, a small enough number so as to have little effect on total vegetation, there was always increased disturbance in groves because stock congregated in the groves in search of shade during summer months. Trampling was severe to understory vegetation and young saplings and low branches were damaged. Similar effects were observed near windmills in sand flats being utilized for grazing.

Four groves were sampled (Table 12) and were found to be almost pure stands of Populus tremuloides. Understory vegetation in groves (Table 13) was similar to that reported by Maini (1960) particularly in herb and shrub sparseness.

Vegetal patterns, similar to those in Table 7, are evident in the Great Sand Hills, when frequency and quadrat-presence are average for the physiographic positions (Table 14). The plants are distributed normally with regard to the gradient represented by the categories. The bimodal tendencies are not as sharply defined as in the Dundurn area and the species concerned differ. Agropyron spp. exhibited a

Table 12. Relative frequency (RF), relative density (RD) and importance value (IV) for trees and shrubs three feet or greater in height in four aspen groves in the Sceptre area.

Species	RF	RD	IV
Populus tremuloides	65	70	135
Populus balsamifera	10	15	25
Salix interior	13	8	21
Salix bebbiana	10	5	15
Populus deltoides var. *occidentalis*	1	1	2
Prunus virginiana	1	1	2
Total	100	100	200

Table 13. Percentage frequency for understory species in four aspen stands in the Sceptre area. Data based on sampling by $\frac{1}{4}$ m^2 quadrats.

Species	Percentage frequency
Juniperus horizontalis	93
Carex heliophila	44
Elaeagnus commutata	29
Symphoricarpos occidentalis	22
Festuca ovina var. *saximontana*	19
Astragalus spp.	13
Psoralea lanceolata	9
Rosa woodsii	9
Solidago missouriensis	7
Juncus balticus	7
Koeleria cristata	6
Vicia sparsefolia	5
Achillea millefolium	3
Artemisia frigida	3
Arctostaphylos uva-ursi	2
Oxytropis macounii	2
Commandra pallida	1
Antennaria microphylla	1
Juniperus communis	1
Smilicina stellata	1
Arabis holboellii	1
Lactuca pulchella	1
Androsace septentrionalis	1
Calamagrostis montanensis	1
Fragaria spp.	1
Galium borale	1

Table 14. Percentage frequency (F) and quadrat-presence (Q-P) for the twenty-five most important species in each of the three selected physiographic categories in the Sceptre area.

Physiographic position	Active complexes		Stabilized dunes		Sand flats	
	% F	% Q-P	% F	% Q-P	% F	% Q-P
Species						
Agropyron spp.	38	26	20	67	32	80
Arabis holboellii	7	13	9	71	8	67
Arctostaphylos uva-ursi	-	-	-	-	7	27
Artemisia campestris	24	66	64	86	9	47
Artemisia cana	-	-	19	33	31	33
Artemisia frigida	8	13	36	67	20	67
Betula occidentalis	-	-	-	-	15	20
Calamovilfa longifolia	28	46	62	52	19	40
Campanula rotundifolia	-	-	13	10	5	27
Carex eleocharis	-	-	-	-	30	7
Carex heliophila	4	13	26	33	43	87
Cerastium arvense	-	-	38	5	-	-
Chrysopsis villosa	20	73	15	90	7	53
Commandra pallida	-	-	18	24	4	27
Corispermum orientale	9	46	-	-	-	-
Elaeagnus commutata	16	20	10	19	21	80
Elymus canadensis	28	86	12	24	3	20
Equisetum hyemale	-	-	25	5	9	13
Festuca ovina var. saximontana	-	-	20	25	9	67
Galium borale	-	-	-	-	3	7
Geum triflorum	-	-	30	5	-	-
Helianthus petiolaris	17	53	3	5	-	-
Juncus balticus	-	-	-	-	11	47
Juniperus communis	3	6	-	-	3	13
Juniperus horizontalis	3	6	31	33	89	87

Table 14 - Continued.

Physiographic position	Active complexes		Stabilized dunes		Sand flats	
	% F	% Q-P	% F	% Q-P	% F	% Q-P
Species						
Koeleria cristata	12	53	53	95	15	80
Lactuca pulchella	9	13	-	-	3	7
Lepidium densiflorum	3	20	15	24	-	-
Linum rigidum	13	46	9	10	6	20
Lithospermum incisum	-	-	9	33	4	20
Lygodesmia juncea	25	60	4	29	5	13
Neomamalaria vivipara	-	-	3	24	5	27
Opuntia fragilis	-	-	3	5	3	7
Oryzopsis hymenoides	27	100	2	5	-	-
Populus balsamifera	-	-	-	-	60	7
Populus deltoides var. occidentalis	-	-	-	-	8	13
Populus tremuloides	-	-	-	-	63	40
Potentilla gracilis	-	-	38	5	-	-
Prunus virginiana	-	-	-	-	26	47
Psoralea lanceolata	85	100	71	95	21	33
Rosa woodsii	10	20	9	19	21	87
Rumex venosus	22	53	10	52	-	-
Salix bebbiana	-	-	-	-	32	47
Salix interior	27	13	-	-	17	20
Salsola kali	4	33	-	-	-	-
Selaginella densa	-	-	5	5	38	13
Shepherdia argentea	-	-	-	-	6	33
Smilicina stellata	-	-	30	24	7	47
Solidago missouriensis	10	40	19	57	15	80
Sporobolus cryptandrus	26	46	29	62	3	7
Stipa comata	6	33	65	100	35	53
Symphoricarpos occidentalis	-	-	13	19	43	67
Vicia sparsefolia	-	-	20	5	10	60

bimodal distribution, occurring frequently on active complexes and also on sand flats. Three shrubs, Salix interior, Elaeagnus commutata and Rosa woodsii were also somewhat bimodal in distribution.

Data presented in Tables 2, 6, 7 and 14 offer several interesting speculations concerning the vegetation on the selected physiographic positions. It is evident that many species reach a peak importance value in one physiographic position, which is in agreement with the concept that organisms respond to single factorial complexes with a normal distribution. If the species distributions are considered as Gaussian curves, then theoretical maximal and minimal distributional points should exist as well as optimal. The tables presented previously indicate that species in the two areas not only have a peak frequency, but also occur in lesser amounts on other physiographic positions. Psoralea lanceolata in the Dundurn area decreased from an importance value of 66 on active complexes to 35 on stabilized blowouts and finally to 9 and 4 on stabilized dunes and dune depressions. Whereas, Calamovilfa longifolia had an importance value of 6 on active complexes, but increased to 15 on stable blowouts and then decreased on the other two physiographic positions. Many other species encountered exhibited similar behavior in importance. The fluctuations in importance value are not as smooth and regular as the theoretical normal curve, which may be due to sharp changes in the environment, an insufficient number of stands, or the relative nature of the importance value index. Regardless, these data do indicate that normal distributions may exist for species in response to the physiographic habitat gradient, although some evidences of bimodal distributions are present.

Compositional Gradient. —— A second means of analyzing phytosociological data excludes any initial reference to habitat categories on which the stands are situated and allows the resolution of many factorial complexes that may be affecting the vegetation. This analysis involves establishment of the degree of phytosociological relationship between the stands, a technique referred to as ordination. The ordination may be accomplished by a variety of objective methods, such as the use of climax adaptation numbers (weighting devices) or direct utilization of coefficients of stand similarity. Once a linear stand ordination has been achieved, some measure of the success of a species (frequency of occurrence, density, height, etc.) may then be plotted against the ordination. This usually yields normal curves, which are considered a response to environmental complexes affecting the vegetation.

Explanation of specific distributional patterns may be accomplished by plotting various environmental characteristics against the stand ordination and observing their behavior along the ordination axis. A repeated coincidence of distributional curves between plants and environmental factors suggests trends in causal agents affecting the vegetation. Correlation coefficients between environmental factors and the ordination may also be calculated to determine the strength of a relationship. It is recognized that factors affecting species are seldom single functioning entities. Conversely, in most cases a multitude of complex and interrelated phenomena affect the vegetation. The techniques of stand ordination permit construction of various axes allowing the study of species distributional patterns in relation to a multi-dimensional system of environmental gradients.

The method applied in ordinating the stands in this study involved the use of similarity coefficients. One means of assessing stand similarity is to apply a single test of similarity between the two samples on the basis of a characteristic exhibited by both samples. It is obvious that such a test, based on only one characteristic, is likely to be inaccurate. A better approach is to apply a series of such tests on a variety of characteristics shared by the samples. The total results can then be used to ascertain the samples that are most closely related.

This technique of similarity analysis can be applied to vegetational stands. If a stand is considered as the total sample, then the specific composition of the stand may be used as a measured characteristic of the sample. A single test of similarity between two stands could be the quantity of Psoralea lanceolata that the stands contain. The accuracy of the similarity measurement is improved by additional testing of the quantity of other species shared by the two stands. In this manner, an accurate measurement of the degree of similarity between two stands is obtained on a floristic basis.

In this study, absolute frequency values of species in each stand were used in the similarity tests. Since the number of quadrats used in the stand sample were equal and any one species had an equal chance of occurring in a stand, all species encountered in the sample were used in the similarity test. The similarity coefficient used in these tests was devised by Motyka et al., (1950) and can be expressed as $C = \frac{2W}{A+B}$ where A is the sum of the frequencies for one stand, B is the similar figure for the second stand and W is the sum of the lesser value for those species common to both stands. Thus, if two stands had exactly the same species present with exactly the same frequency value then C would equal 1.00, since A and B would be equal and both would equal W. Conversely, if two stands had no species in common C would equal 0. These indices are usually converted to whole numbers by multiplying the index by 100, giving a range of similarities from 0 to 100. Absolute values were used in the calculations since conversion to relative values might obscure differences between stands for a given species, particularly if the sum of the frequencies was very much different for the two stands.

When a large number of stands are to be compared, each with every other stand, the calculations required become numerous, since there are $n \times \frac{n-1}{2}$ comparisons to be made. Thus, for 10 stands 45 comparisons are needed and for larger numbers of stands the number of comparisons becomes increasingly greater.

In this study, separate matrices were constructed for the Dundurn and Sceptre areas, showing the similarity coefficients between each stand and every other stand within the same study area. Separate matrices were constructed, since combining the stands into one matrix was prohibited by the increase in calculations involved. Table 15 is an example of the matrix constructed for the Dundurn area, giving the coefficients between 20 stands. In the actual analysis, a total of 52 and 49 stands required calculation of 1,326 and 1,176 separate coefficients for the Dundurn and Sceptre study areas, respectively. The next step was to sum the coefficients for each stand. The stand with the lowest sum was then considered to be the most different from all the other stands in the same area and was used as the initial reference stand of the primary or "X" axis of the ordination. The other

Table 15. Matrix of similarity coefficients for twenty stands in the Dundurn area.

Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	–	44	25	40	15	20	20	5	25	25	19	24	21	9	16	23	8	0	0	16
2	–	–	9	23	32	28	26	21	34	30	29	43	21	19	29	28	15	14	20	25
3	–	–	–	32	5	3	3	7	10	6	7	5	3	6	9	7	7	1	2	12
4	–	–	–	–	5	3	2	6	12	6	13	5	3	6	9	7	7	0	1	19
5	–	–	–	–	–	52	51	31	35	54	72	60	59	65	54	65	57	35	30	19
6	–	–	–	–	–	–	83	45	49	77	64	68	72	68	59	73	54	41	37	32
7	–	–	–	–	–	–	–	38	45	73	64	60	65	64	54	68	49	44	40	27
8	–	–	–	–	–	–	–	–	13	29	23	25	18	22	15	24	14	58	67	57
9	–	–	–	–	–	–	–	–	–	51	49	54	45	49	55	51	39	13	14	14
10	–	–	–	–	–	–	–	–	–	–	61	69	62	59	63	62	44	34	33	17
11	–	–	–	–	–	–	–	–	–	–	–	60	51	58	62	53	52	26	24	15
12	–	–	–	–	–	–	–	–	–	–	–	–	63	61	73	62	46	24	31	18
13	–	–	–	–	–	–	–	–	–	–	–	–	–	57	66	60	45	30	26	14
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	73	56	55	31	26	16
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	58	58	19	15	15
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	47	33	28	19
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	17	10
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	74	38
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	43
20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

end of the primary axis was the stand having the least similarity to the initial reference stand. Since the reference stands were chosen on the basis of dissimilarity and the subsequent positioning of all the other stands was on the basis of dissimilarity to the reference stands, inverse values of the coefficients of similarity were obtained by subtracting the coefficients from 100. Thus, two stands with no species in common would be 100 units dissimilar, while identical stands would be 0 units dissimilar. The initial ordination axis was then calculated from the matrices of dissimilarity values.

The ordination technique used is based on the concept that the degree of phytosociological relationship (dissimilarity) between stands can be used to place these stands in an objective linear order. The ordination attempts to extract from a disordered matrix of interstand similarity coefficients, an ordinated spatial pattern in which the interstand distance is related to their degree of similarity.

The procedure by which the first ordination of the stands (X axis) was achieved is based on the supposition that given a set of values representing distances between points, it is possible to ascertain the spatial positions of a given point by the use of reference points separated by the greatest distance. The method used in this study was developed by Bray and Curtis (1957) and later modified by Beals (1960). Only figures for the Dundurn ordination will be used in illustrating the linear positioning of the stands, since the procedure was identical for both areas.

The length of the X axis in the Dundurn area was 100 dissimilarity units, stands 4 and 45 having 0 similarity. Each of the other stands was located along this axis by means of an equation involving the

Pythagorean theorem. If arcs representing the dissimilarity of a particular stand from each reference stand are drawn from the reference stands, they will intersect above the axis line (Fig. 13). A perpendicular can then be drawn from the intersection to the axis, thus projecting the location of the stand onto the axis. In this study, the arcs were not drawn, but instead a formula derived by Beals (1960) was used in computing stand positions on the axis. The formula is based on the presence of two right triangles in Fig. 13, with sides exD_4 and $e(L-x)D_{45}$. The length of each hypotenuse is equal to the dissimilarity of a given stand to each reference stand. One side, (e), of the triangles is equal, and the sum of the third side of both triangles is known to be L, the total length of the axis. Thus, the triangles have the equations: $e^2 + x^2 = D_4{}^2$

$$e^2 + (L-x)^2 = D_{45}{}^2$$

By solving for x, which would represent the stand position on the axis, a calculating formula results:

$$x = \frac{L^2 + D_4{}^2 - D_{45}{}^2}{2L}$$

This formula allows objective positioning of stands along the X axis on the basis of dissimilarity to the selected reference stands. When the positions were calculated (Table 16), they could then be plotted on the axis in a linear order.

Dundurn

In order to study the behavior of a particular species along the ordination axis, frequency values for the species were first plotted on the axis. These values were then averaged by 10 unit intervals of the

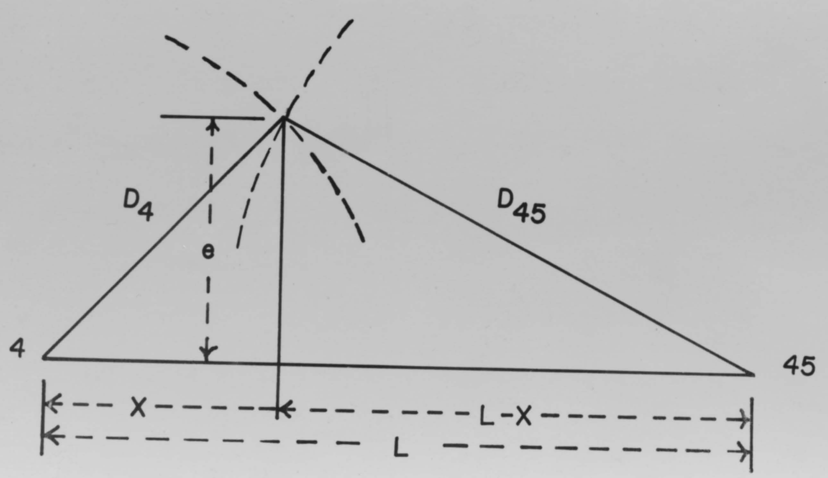

Fig. 13. Illustration of stand location along the ordination axis, by projection of arc intersection. 4 and 45 are initial reference stands, L is the dissimilarity value between the reference stands, D_4 and D_{45} are dissimilarity values of a given stand from the reference stands and X is the location of the stand along the axis.

Table 16. Stand positions on the X and Y ordination axes in the Dundurn area.

Stand No.	Ordination Axis X	Ordination Axis Y	Stand No.	Ordination Axis X	Ordination Axis Y
1	37.6	18.3	27	44.7	72.7
2	52.2	29.8	28	58.5	87.0
3	24.1	32.5	29	66.9	56.1
4	0.0	30.5	30	53.5	63.9
5	75.9	37.9	31	40.7	71.9
6	76.5	44.0	32	59.9	57.5
7	82.3	34.3	33	51.6	63.5
8	53.6	76.3	34	75.2	59.5
9	64.2	0.0	35	79.7	66.3
10	80.6	26.6	36	79.3	26.8
11	65.4	51.8	37	71.3	64.0
12	79.4	32.8	38	79.2	47.3
13	81.3	26.8	39	84.0	40.2
14	74.9	25.2	40	90.8	53.8
15	72.8	25.3	41	83.3	45.3
16	83.1	28.3	42	71.9	34.6
17	67.3	24.3	43	91.7	43.5
18	65.5	73.7	44	91.2	35.1
19	62.8	72.7	45	100.0	23.4
20	46.6	71.0	46	84.9	35.4
21	76.2	60.2	47	24.0	18.3
22	62.9	43.5	48	27.9	17.5
23	83.2	35.7	49	31.0	18.8
24	75.7	27.3	50	29.7	15.0
25	60.6	65.0	51	14.9	27.5
26	42.2	73.4	52	28.3	21.4

axis, the averages plotted on graph paper and connected by straight lines. Figure 14 illustrates such distributional curves along the X axis for 24 important species in the Dundurn area. Several important features are evident in these graphs. Firstly, the species exhibit askew normal curves or portions of such curves. Such behavioral patterns serve as an indication of the ecological amplitude of the plants, since organisms usually respond to their complex environment with a normal distribution having maximal, minimal and optimal points. Such points are evident for species plotted on the X axis.

Secondly, the species have peak frequencies throughout the axis. The species in the left column peak towards the left of the axis, those in the middle column peak near the middle of the axis and the right column contains species peaking towards the right of the X axis. This indicates the wide variation in tolerances exhibited by the plants in relation to the gradient represented by the axis, with no evidence that the tolerances are identical for any two species. The curves are often similar, but there is usually some difference, either in distribution or magnitude.

A third feature of Fig. 14 is that it supports the concept of a vegetational continuum. If all the species were presented on one axis, there would be extensive overlapping of distributions.

Inspection of the behavior of particular species along the X axis (Fig. 14) shows that Psoralea lanceolata, Helianthus petiolaris, Lygodesmia juncea and Oryzopsis hymenoides are the most frequent species towards the left of the axis. Psoralea and Lygodesmia, however, extend their ecological range over the entire gradient, while Oryzopsis and Helianthus are restricted in their amplitude.

Fig. 14. The phytosociological behavior of 24 principal species along the X ordination axis in the Dundurn area. The species are:

1. *Psoralea lanceolata*
2. *Helianthus petiolaris*
3. *Lygodesmia juncea*
4. *Oryzopsis hymenoides*
5. *Corispermum orientale*
6. *Sporobolus cryptandrus*
7. *Artemisia campestris*
8. *Calamovilfa longifolia*
9. *Selaginella densa*
10. *Carex eleocharis*
11. *Artemisia frigida*
12. *Stipa comata*
13. *Koeleria cristata*
14. *Chrysopsis villosa*
15. *Phlox hoodii*
16. *Bouteloua gracilis*
17. *Carex heliophila*
18. *Artemisia ludoviciana*
19. *Agropyron* spp.
20. *Juniperus horizontalis*
21. *Solidago missouriensis*
22. *Symphoricarpos occidentalis*
23. *Prunus virginiana*
24. *Rosa woodsii*

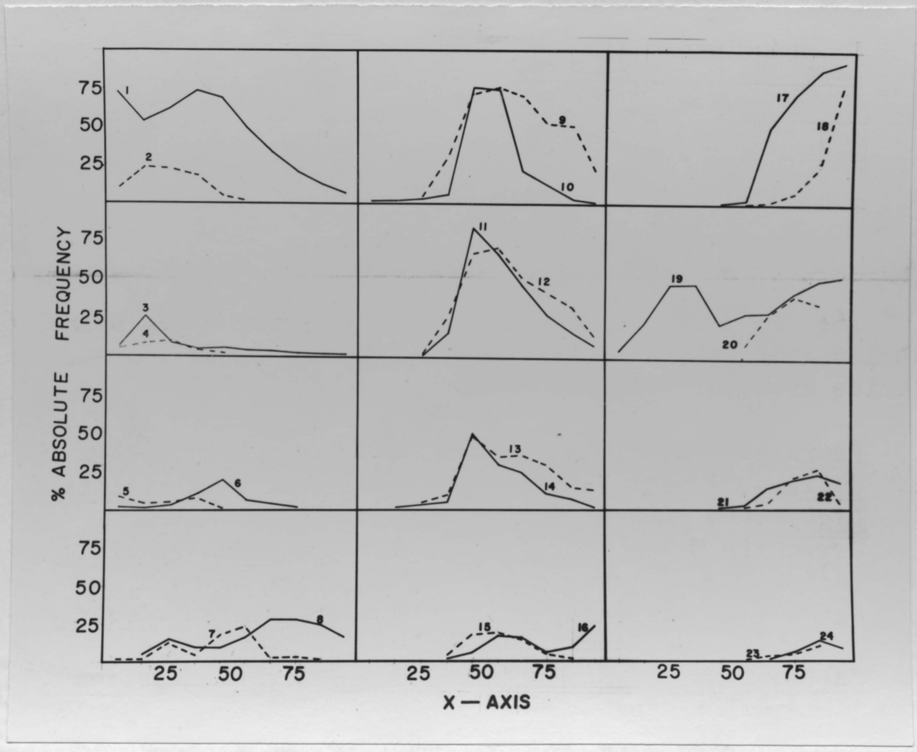
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Fig. 14.

The middle of the X axis is the peak area for *Carex eleocharis*, *Selaginella densa*, *Stipa comata* and *Artemisia frigida*. *Carex eleocharis* is the only species having an ecological amplitude, which extends to the left of the X axis, but all four species were commonly found to the right. The species in the two lower graphs of the middle column occur less frequently in the middle of the axis, but more frequently towards the right.

The right of the X axis (Fig. 14, right column) has *Carex heliophila* and *Artemisia ludoviciana* as the most frequent species. Two other species are also important, but have a tendency to occur in stands located towards the left of the axis or to reach their peak frequency slightly before the extreme right. *Juniperus horizontalis* is an example of a plant with its optimum development towards the right of the axis, but peaking in frequency on the graph and not forming just a portion of a normal curve as do *Carex heliophila* and *Artemisia ludoviciana*. Closely associated with *Juniperus horizontalis* and its distribution is *Agropyron* spp. The behavioral curves of this complex grass genus are interesting in that they appear to be bimodal. The first mode is towards the left on the axis, while a second occurs to the right of center. Identification of specific members of this genus is extremely difficult in the vegetative state, which may account for the bimodal curve, since the curve may represent several species. Ecotypical differentiation could also be responsible. Although most of the species curves along the X axis in the Dundurn area were normal with respect to environmental gradients presented by the axis, it is probable that other factors may be affecting the vegetation. Such a bimodal distribution could result from more than one factor affecting the vegetation as well as the taxonomic difficulties.

Because of the bimodal situation, a second factorial complex was suspected. In order to reveal the presence of a second environmental gradient, it was necessary to construct a secondary ordination axis. Presentation of species distributions along an ordinated stand axis in a one-dimensional view does not reveal whether the frequency peaks are in the same plane. This is similar to looking at a mountain range and not being able to discern the near from the far peaks (Curtis 1959). One means of distinguishing the plane of distribution is to extract a second stand ordination (Y axis) and study species behavior in relation to both axes. The procedure for obtaining the secondary axis is the same as that in the primary axis construction. The Y axis ordination is thus an attempt to separate stands close together on the X axis that are actually floristically different. Such an ordination will place the stands in a spatial plane with reference to both axes (Table 16).

Figure 15 shows the location of each Dundurn stand in relation to the X and Y axes. It is evident that the one dimensional view in Figure 14 did not represent the actual placement of the curves, since plotting of the stands in two dimensions separated some stands further away from the X axis; *e.g.*, those above 48 on the Y axis. This type of graphic portrayal of stand positions is similar to viewing a normal curve from above. Of course, with such a view it is impossible to say whether or not the stands are all in the plane represented by the two axes. This could only be ascertained by the resolution of a third or Z axis.

Figures 16 and 17 illustrate a two dimensional ordination with

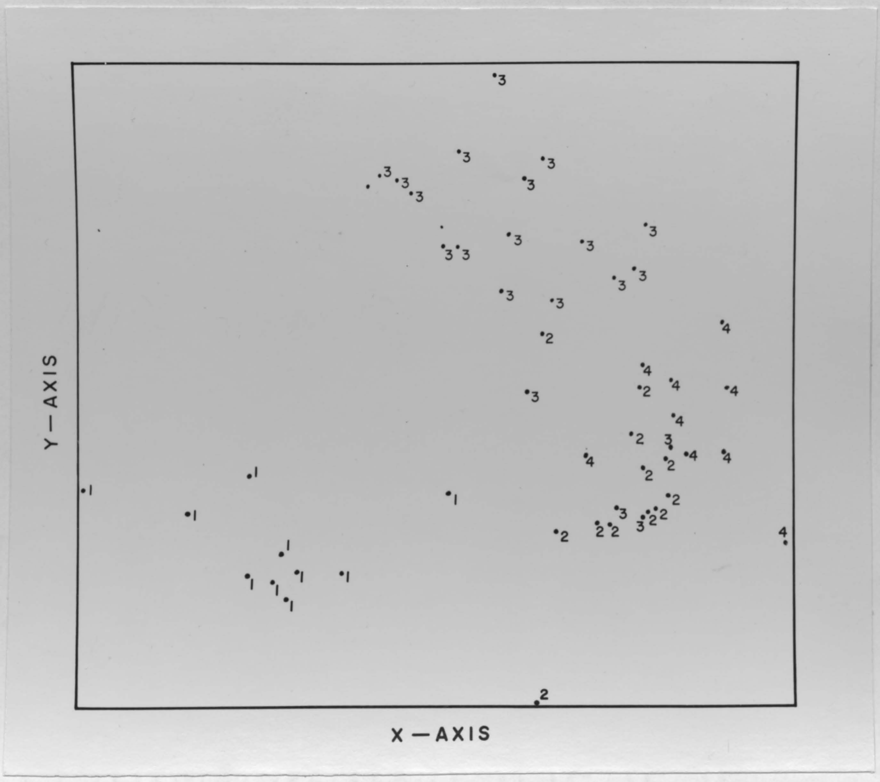


Fig. 15. The distribution of stands within the Dundurn X-Y ordination according to physiographic position. 1 = active complexes, 2 = stabilized blowouts, 3 = stabilized dunes and 4 = dune depressions.

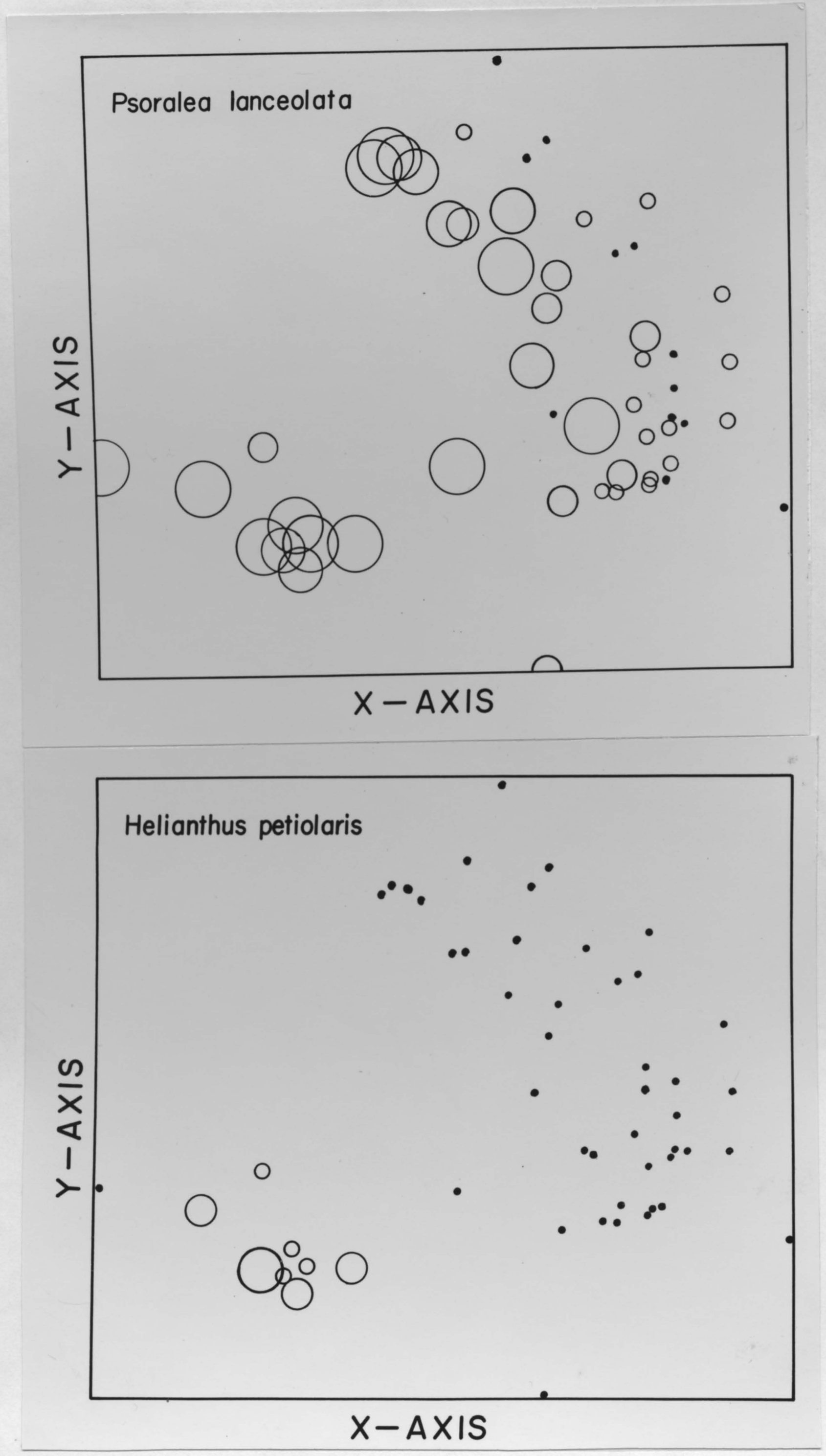


Fig. 16. Phytosociological behavior of two species, which had high frequency at the left of the X axis (Fig. 14), within the Dundurn X-Y ordination.

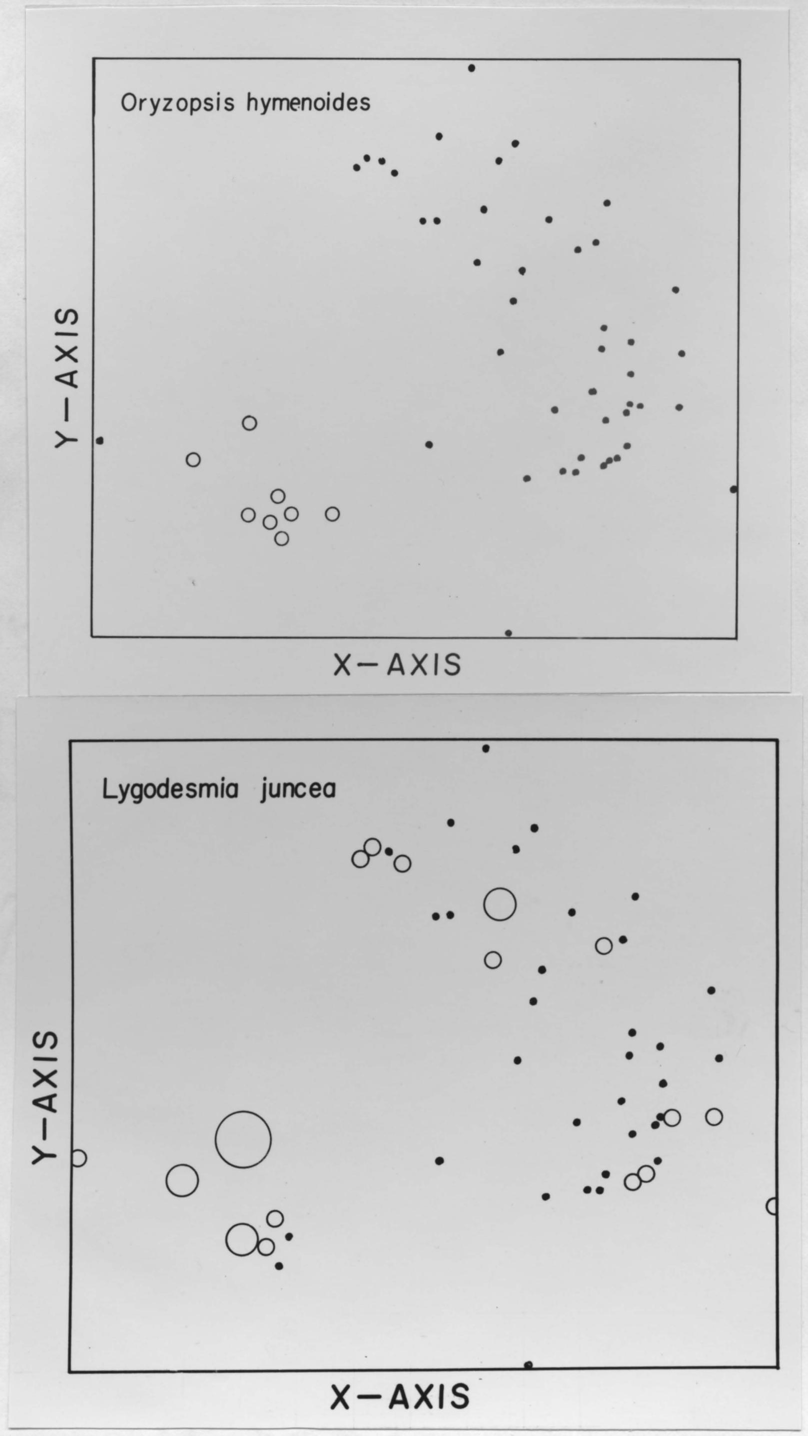


Fig. 17. Phytosociological behavior of two species, which had high frequency at the left of the X axis (Fig. 14), within the Dundurn X-Y ordination.

frequency of four species plotted on the ordinations. The center of each circle is at a stand location, and the size of circle represents absolute frequency for the particular species in the stand. Frequency values of 75 or more are shown by the largest circle (see Fig. 18), values from 50 to 74 by the next smaller circle, values from 25 to 49 by the next size circle and values from 1 to 24 by the smallest circle. Stands where the species portrayed was absent in the quadrat sample are indicated by dots. Such a presentation of behavioral patterns is useful in determining the area of importance for a species with reference to the environmental complexes represented by the ordination axes. Figures 16 and 17 also indicate that the species have their center of activity in particular portions of the total graph area. Of course, the area enclosed by the X and Y coordinates does not include all the theoretically possible stand positions.

It is obvious, nevertheless, that between the stands sampled there are differences in frequency and distribution. Psoralea lanceolata, for example, is wide ranging in its distribution, with two centers of high frequency (in the lower left and upper center). Helianthus petiolaris and Oryzopsis hymenoides, however, are restricted to the lower left of the graph and are low in frequency even within their environmental optimum. Lygodesmia juncea is more ubiquitous in its distribution than the above species, but attained high frequency in only two stands. The highest frequency values are usually clustered in a small area and decrease towards the periphery of the species' distribution.

Figures 18 and 19 similarly illustrate that high frequency values for a species are usually clustered, with decreases in value as the

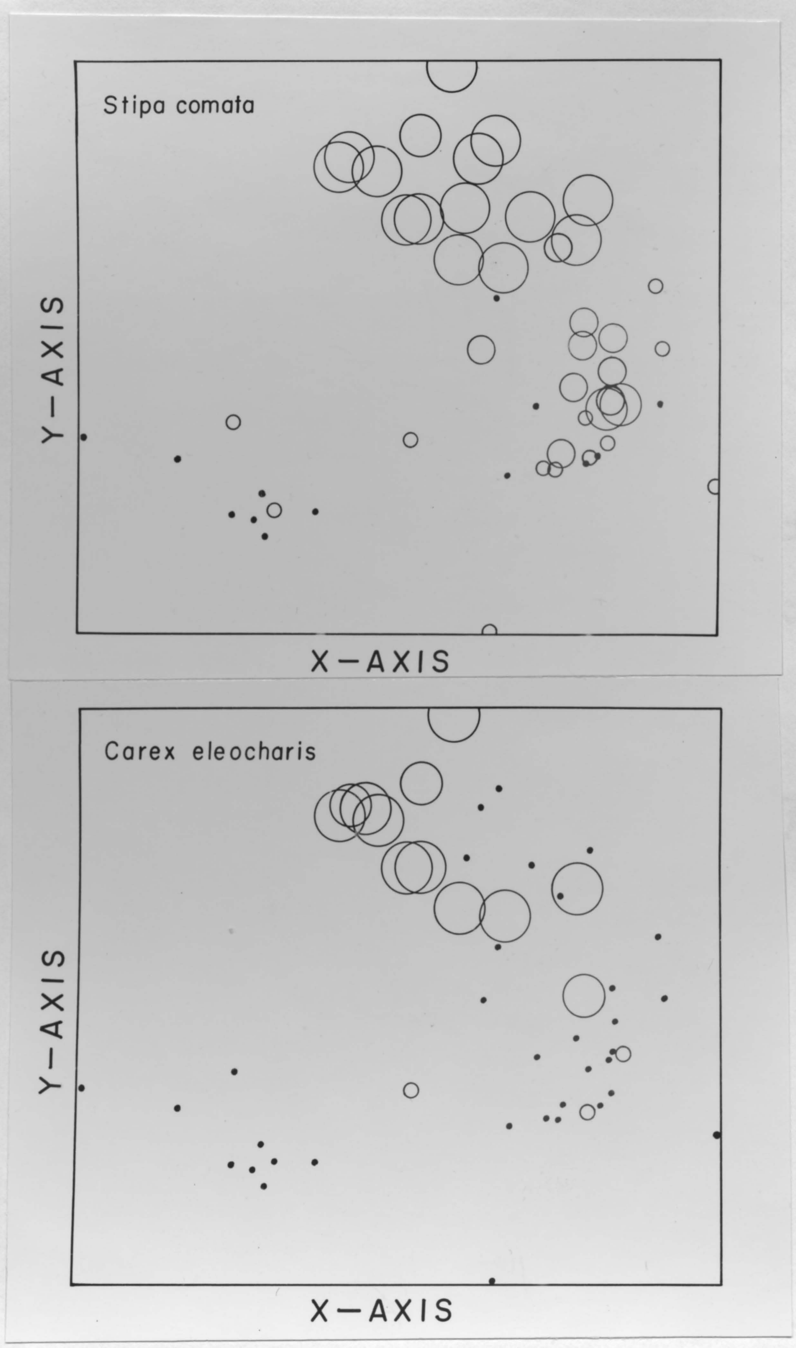


Fig. 18. Phytosociological behavior of two species, which had high frequency at the middle of the X axis (Fig. 14), within the Dundurn X-Y ordination.

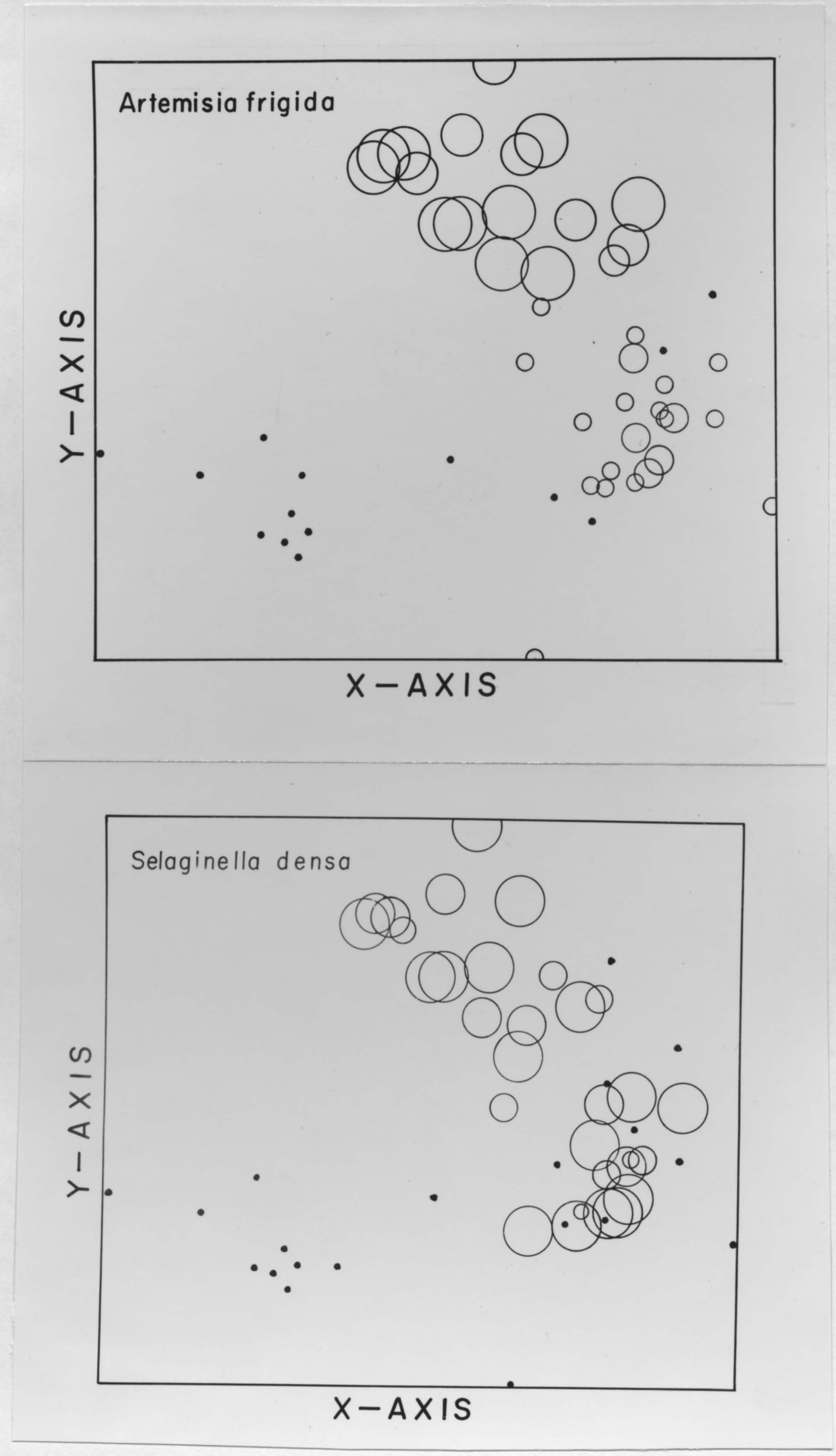


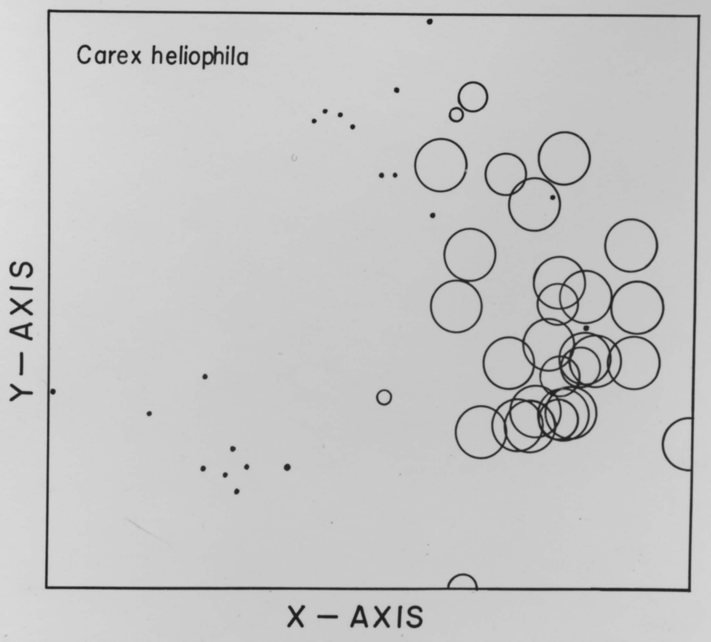
Fig. 19. Phytosociological behavior of two species, which had high frequency at the middle of the X axis (Fig. 14), within the Dundurn X-Y ordination.

edge of the measured distribution is approached. Of the species in Figures 18 and 19, only Stipa comata is found in the lower left of the graph and this was at a low frequency. Three species, Artemisia frigida, Stipa comata and Carex eleocharis, have high frequency values in the upper center. Selaginella densa, a small club-moss abundant in the Canadian Mixed Prairie (Coupland 1950), was high in frequency in almost all stands except those occurring in the lower left of the graph.

Some species have their center of greatest frequency in the middle right of the graph (Figs. 20 and 21). Artemisia ludoviciana var. gnaphalodes was restricted to these stands, attaining high frequency in some stands and low frequency in others. Carex heliophila was the most frequent species in stands at the middle right of the graph, often occurring with frequencies of 80% to 95%. A third species, Juniperus horizontalis, was restricted to fewer stands than Carex heliophila, but was very frequent where present.

The two dimensional distribution of Agropyron spp. is interesting in that the bimodal tendency, discussed in reference to the primary axis, is clearly evident. This taxon appears to have two centers of activity; in the lower left and in the middle right of the X - Y graph.

The two-dimensional view of the species distributions indicates that the initial axis representation (Fig. 14) did not portray the proper spatial order of all species involved, with reference to affecting gradients. Some of the frequency peaks on the X axis were evidently in different planes due to other factorial agents operating in the environment of the vegetation.



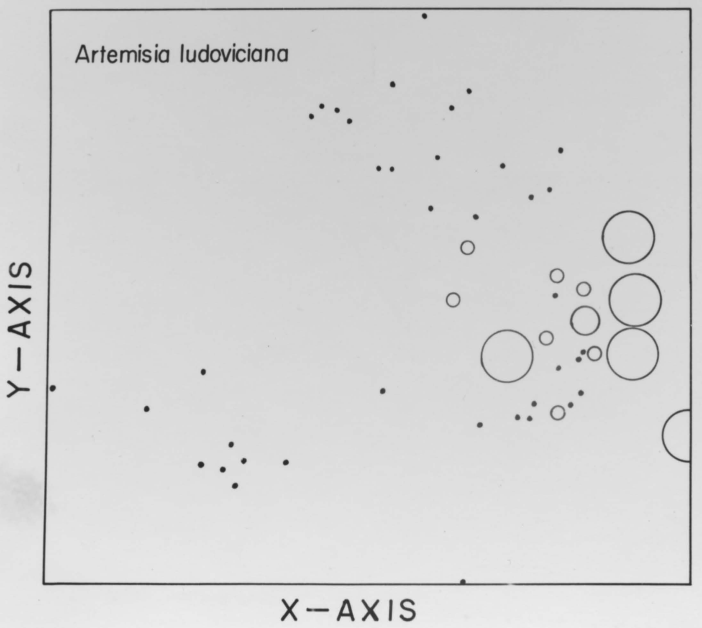


Fig. 20. Phytosociological behavior of two species, which had high frequency at the right of the X axis (Fig. 14), within the Dundurn X-Y ordination.

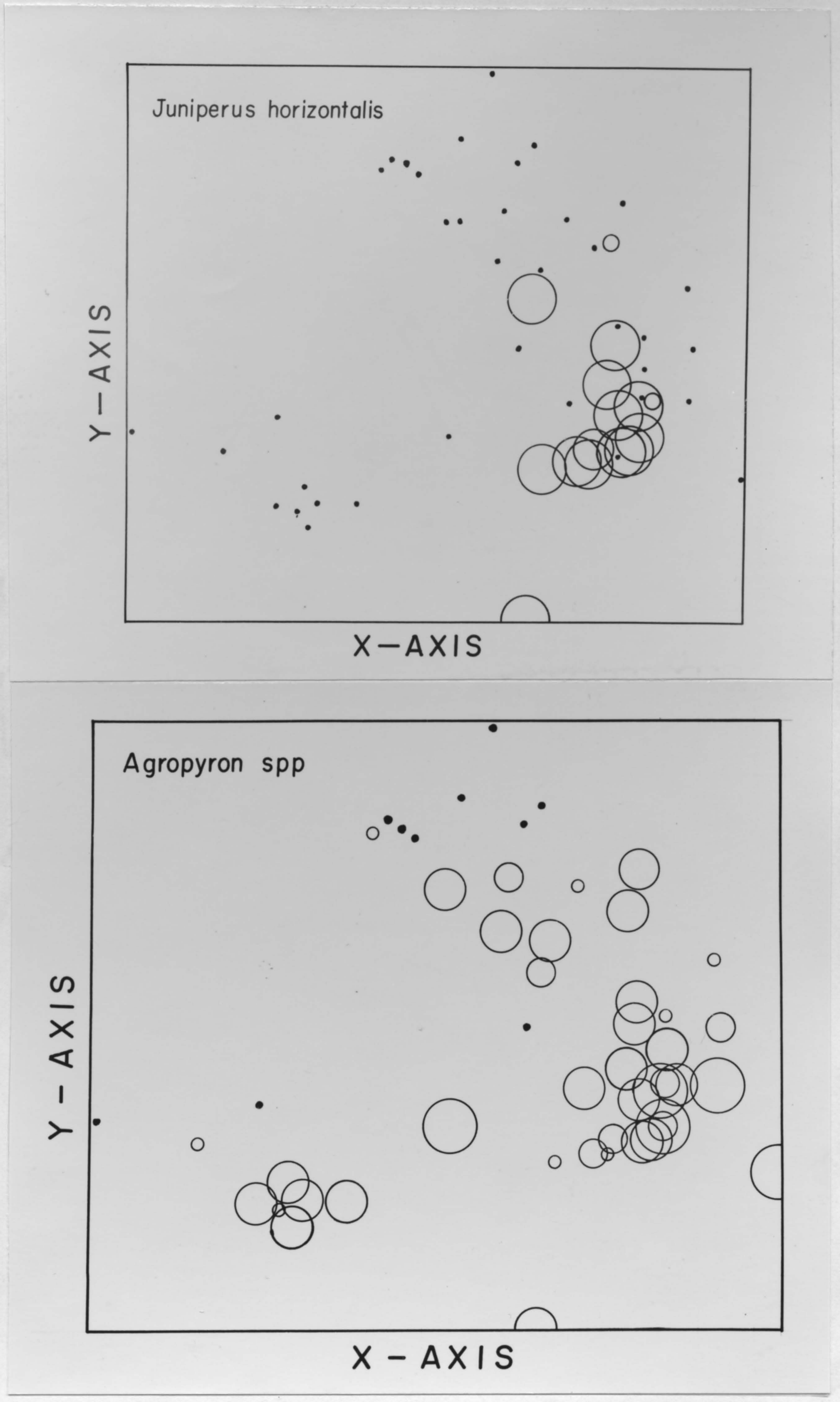


Fig. 21. Phytosociological behavior of two species, which had high frequency at the right of the X axis (Fig. 14), within the Dundurn X-Y ordination.

Sceptre

X - Axis. —— Stands sampled in the Sceptre area were ordinated in the manner described for the Dundurn area. The X and Y axis positions are given in Table 17. Frequency values plotted against the X axis again yielded normal curves (Fig. 22), with species peaking in frequency throughout the axis. Psoralea lanceolata exhibited a similar curve to the one in the Dundurn area except that it was more frequent at the left on the Sceptre X axis. Artemisia campestris also attained a high frequency in the same segment of the axis. The remaining six species in the left column are prominent at the left of the axis, but of lower frequency. Artemisia cana did, however, reach its peak in frequency at about 50 on the X axis, which is further to the right than any other species in the left column.

The middle column in Figure 22 indicates those species attaining highest frequency near 50 on the X axis. Stipa comata, Koeleria cristata, and Calamovilfa longifolia are wide ranging in distribution over the X axis, but except for the center of the axis they are not important constituents of the vegetation. Agropyron spp. did not exhibit the bimodal tendency as in the Dundurn area, but peaked in frequency only to the right of Stipa comata, Calamovilfa longifolia. Solidago missouriensis, a species of low frequency, attained its peak in the same area as Agropyron spp. The two plants in the bottom graph, middle column, indicate a definite shift towards the right portion of the axis in their ecological amplitude.

An inspection of the right column in Figure 22 reveals the behavioral patterns of eight species in the Sceptre area that attain

Table 17. Stand positions on the X and Y ordination axes in the Sceptre area.

Stand No.	Ordination Axis		Stand No.	Ordination Axis	
	X	Y		X	Y
1	75.9	38.1	26	23.4	18.2
2	73.0	38.6	27	22.8	33.4
3	16.2	14.4	28	21.1	19.6
4	24.1	25.4	29	9.3	32.8
5	21.7	30.0	30	14.4	46.2
6	5.2	11.2	31	21.4	36.7
7	50.6	1.6	32	0.0	32.7
8	19.2	14.3	33	6.4	9.3
9	27.3	2.3	34	5.4	24.5
10	18.6	10.0	35	13.5	27.7
11	10.5	23.5	36	10.6	14.6
12	11.5	31.4	37	91.9	52.2
13	22.4	22.7	38	80.4	42.1
14	54.9	21.9	39	77.7	40.1
15	86.5	39.7	40	7.7	31.3
16	33.6	0.0	41	85.4	39.5
17	16.4	13.2	42	100.0	36.5
18	19.6	8.3	43	22.1	31.7
19	83.0	31.3	44	40.0	34.5
20	24.4	8.0	45	50.0	30.0
21	15.0	5.7	46	55.2	40.8
22	10.1	34.2	47	85.0	31.4
23	36.5	42.5	48	70.8	42.3
24	25.7	49.6	49	74.2	59.0
25	35.9	60.0			

Fig. 22. The phytosociological behavior of 24 principal species against the X ordination axis in the Sceptre area. The species are:

1. Psoralea lanceolata
2. Artemisia campestris
3. Elymus canadensis
4. Chrysopsis villosa
5. Oryzopsis hymenoides
6. Lygodesmia juncea
7. Sporobolus cryptandrus
8. Artemisia cana
9. Stipa comata
10. Koeleria cristata
11. Calamovilfa longifolia
12. Agropyron spp.
13. Artemisia frigida
14. Solidago missouriensis
15. Festuca ovina var. saximontana
16. Carex heliophila
17. Juniperus horizontalis
18. Symphoricarpos occidentalis
19. Populus tremuloides
20. Salix bebbiana
21. Rosa woodsii
22. Betula occidentalis
23. Elaeagnus commutata
24. Prunus virginiana

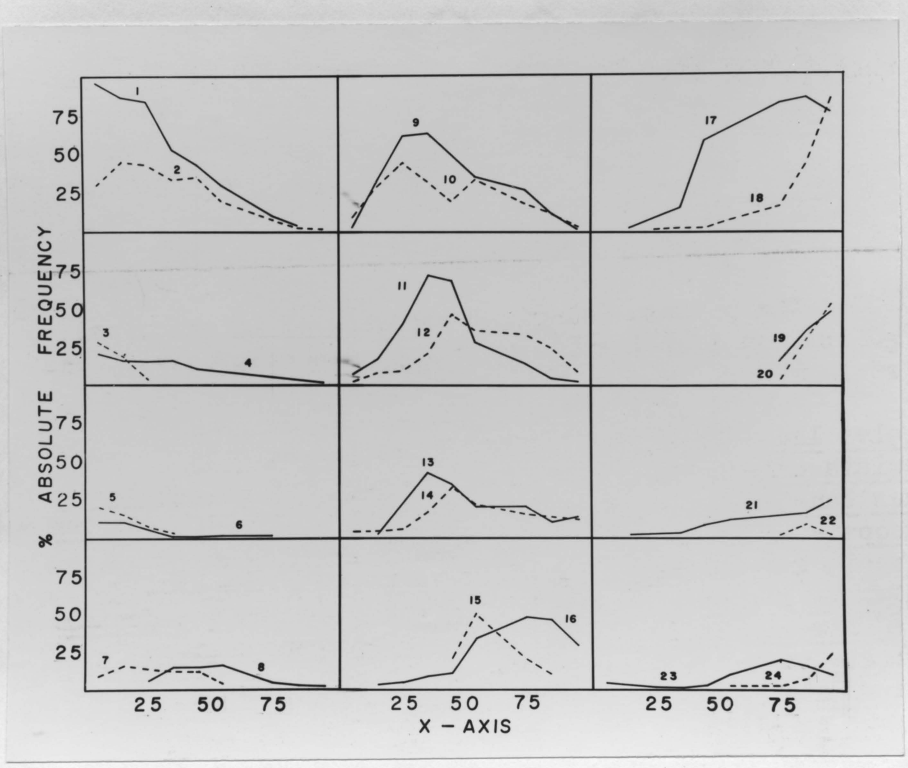

% ABSOLUTE FREQUENCY
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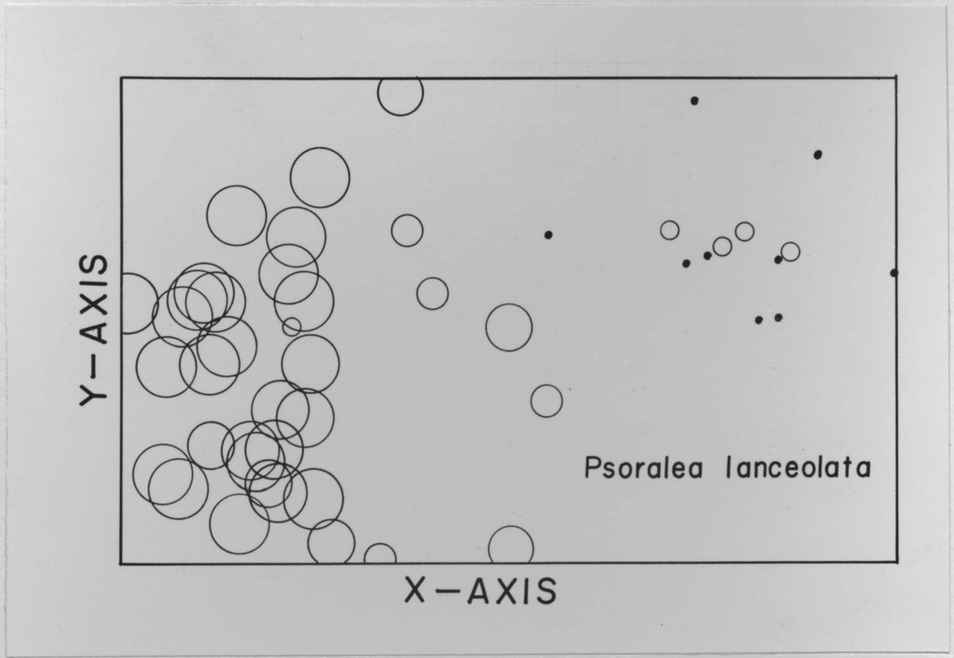
Fig. 22.

peak frequency towards the right on the X axis. The most important of these are Juniperus horizontalis and Symphoricarpos occidentalis. Populus tremuloides and Salix bebbiana are also present in varying amounts at the extreme right on the X axis, and are accompanied by a variety of shrubs. Some of the shrubs are restricted to the right (Elaeagnus commutata), while a few are more ubiquitous (Rosa woodsii and Prunus virginiana). Betula occidentalis, a small tree, only occurred in stands at the right on the axis.

The behavioral curves in Figure 22, again show a continuous distribution of species in relation to the initial axis. It is impossible, however, with a one dimensional view of the curves, to ascertain if they are all in the same plane. Therefore, a secondary axis was constructed in an attempt to resolve other factors affecting the vegetation.

Y - Axis. —— There was not a marked separation of the Sceptre stands upon placement on the X - Y coordinates. Figures 23 and 24 show the distributional patterns for species that have their peak frequency in the lower left. Psoralea lanceolata was found on a large number of stands, but the center of greatest activity was to the extreme left of the X axis and low on the Y axis. Frequency values of Psoralea decrease with movement towards the right on the axis, some stands showing a complete absence of the species. Elymus canadensis also occurred in the lower left, but with considerably lower frequency values than Psoralea and exhibited considerably more restriction, suggesting a narrow ecological tolerance. Artemisia campestris had a high center of activity further to the right and had as a closely associated species, Chrysopsis villosa. Neither of these



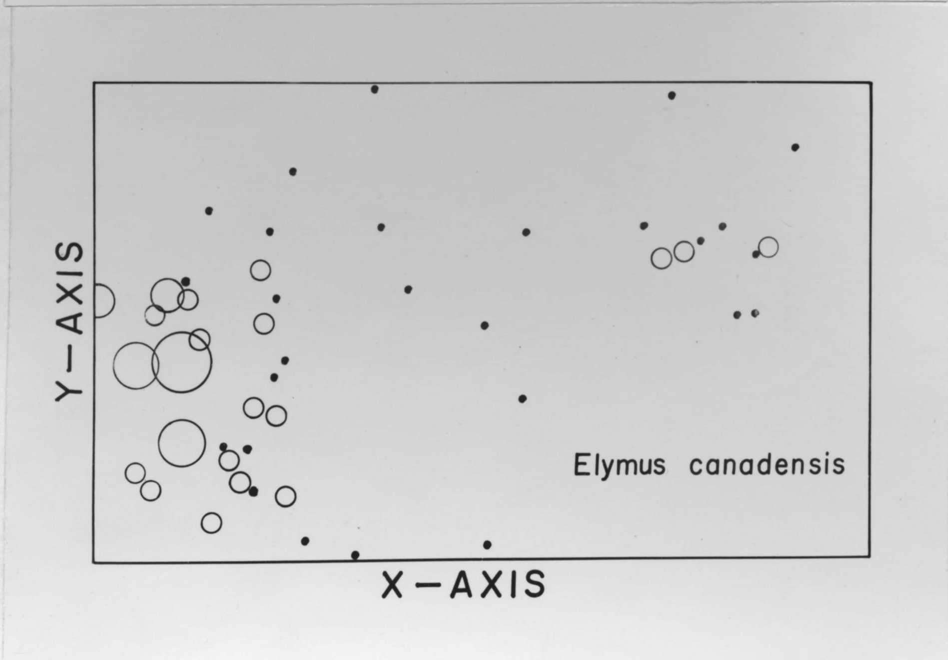


Fig. 23. Phytosociological behavior of two species, which had high frequency towards the left of the X axis (Fig. 22), within the Sceptre X-Y ordination.

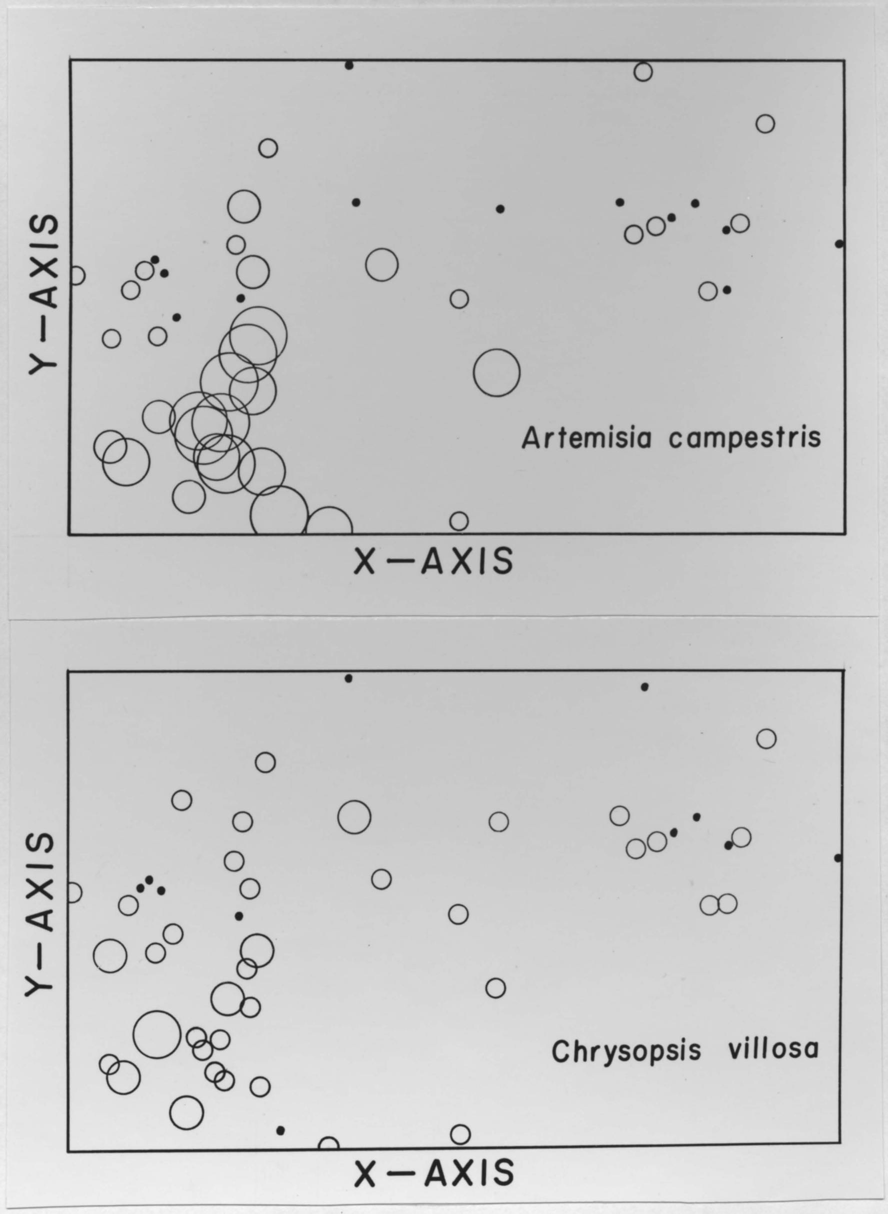


Fig. 24. Phytosociological behavior of two species, which had high frequency towards the left of the X axis (Fig. 22), within the Sceptre X-Y ordination.

species was important in stands occurring at the right side of the graph.

Nevertheless, many species did have high frequency values at the right (Figs. 25 and 26). *Stipa comata*, *Koeleria cristata* and *Calamovilfa longifolia* have distributional ranges towards the right, although their highest frequencies are still at the left. *Juniperus horizontalis*, which was not frequent in stands located to the left, had high frequency in stands located to the right.

Figures 27 and 28 are the behavioral patterns of four additional species in the Sceptre area, those having their greatest frequency towards the right middle of the graph. *Carex heliophila* is the widest ranging of the four, followed by *Symphoricarpos occidentalis*, *Salix bebbiana*, and *Populus tremuloides*. The last species mentioned had its only occurrence and highest frequency in stands towards the right in the graph. *Salix bebbiana* often occurred in the same stands, but with lower frequency.

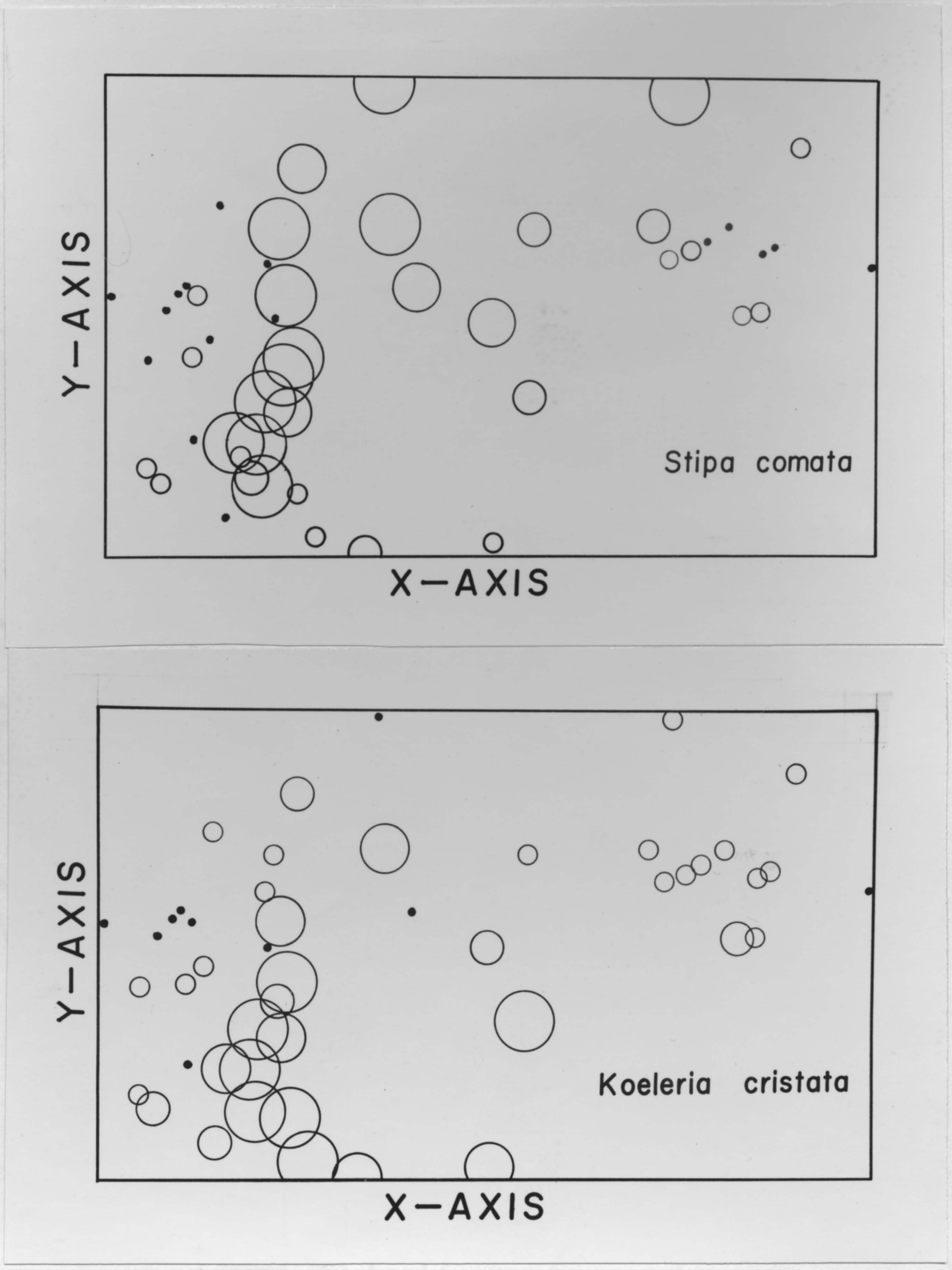


Fig. 25. Phytosociological behavior of two species, which had high frequency in the middle of the X axis (Fig. 22), within the Sceptre X-Y ordination.

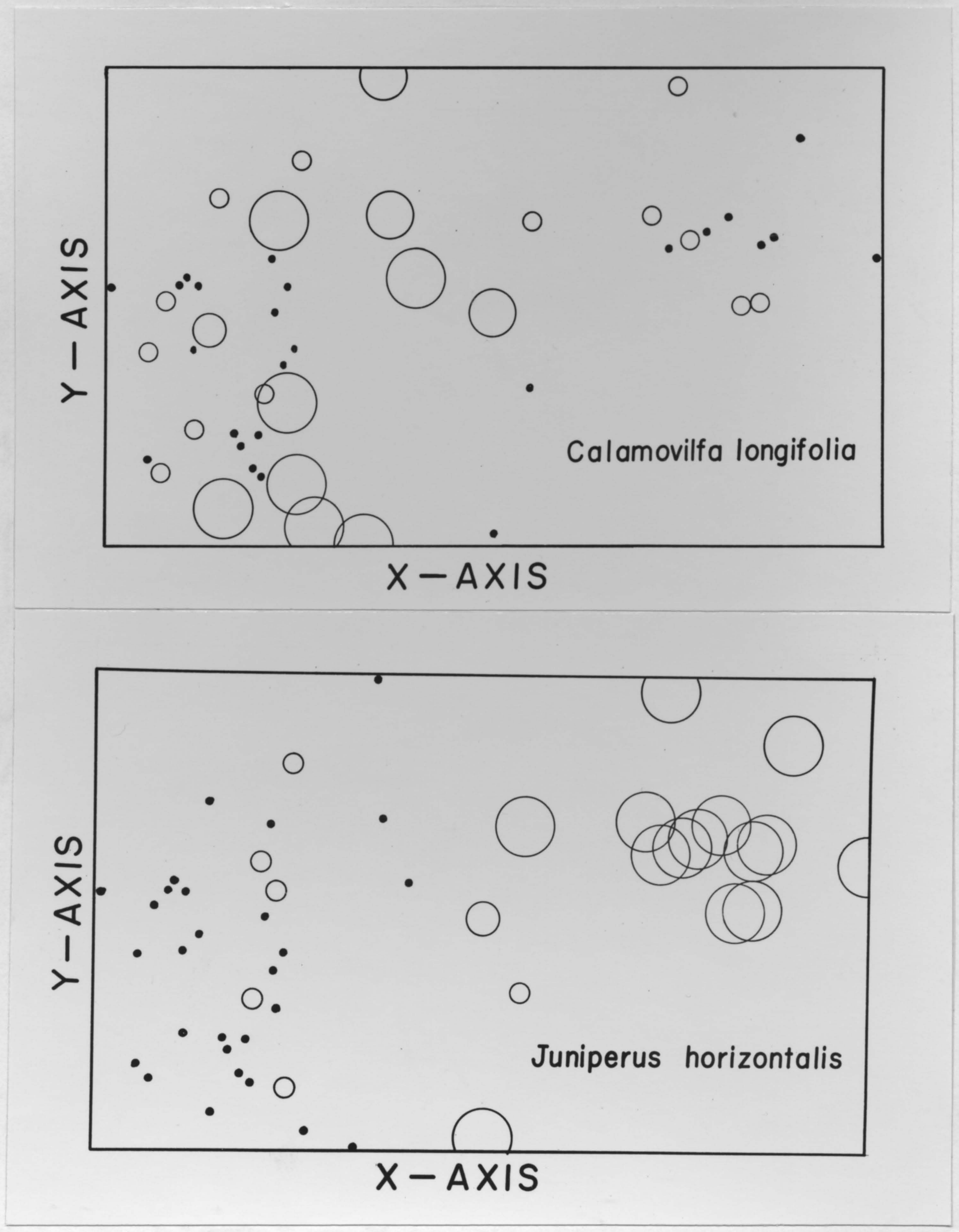
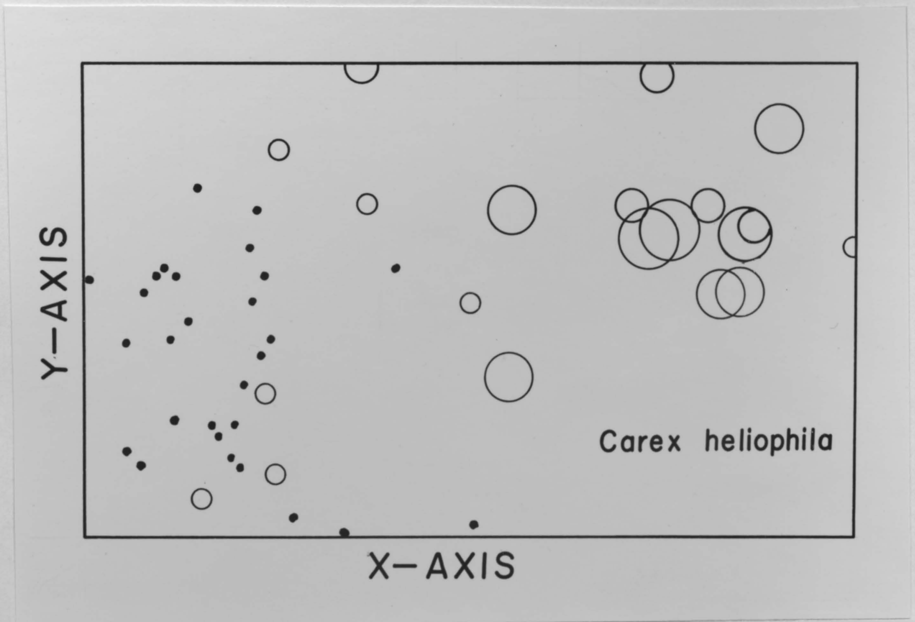


Fig. 26. Phytosociological behavior of two species, which had high frequency in the middle of the X axis (Fig. 22), within the Sceptre X-Y ordination.



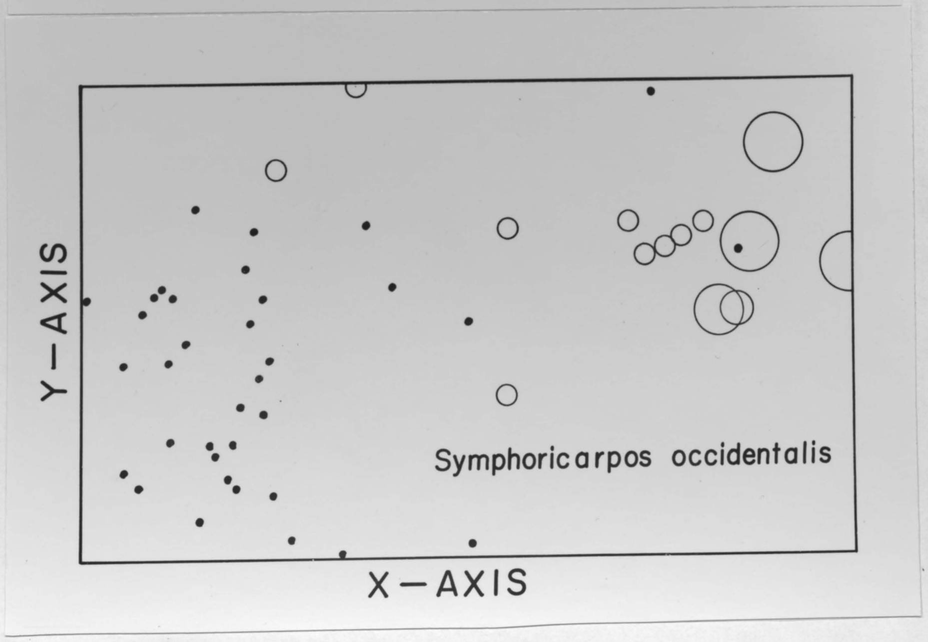


Fig. 27. Phytosociological behavior of two species, which had high frequency towards the right of the X axis (Fig. 22), within the Sceptre X-Y ordination.

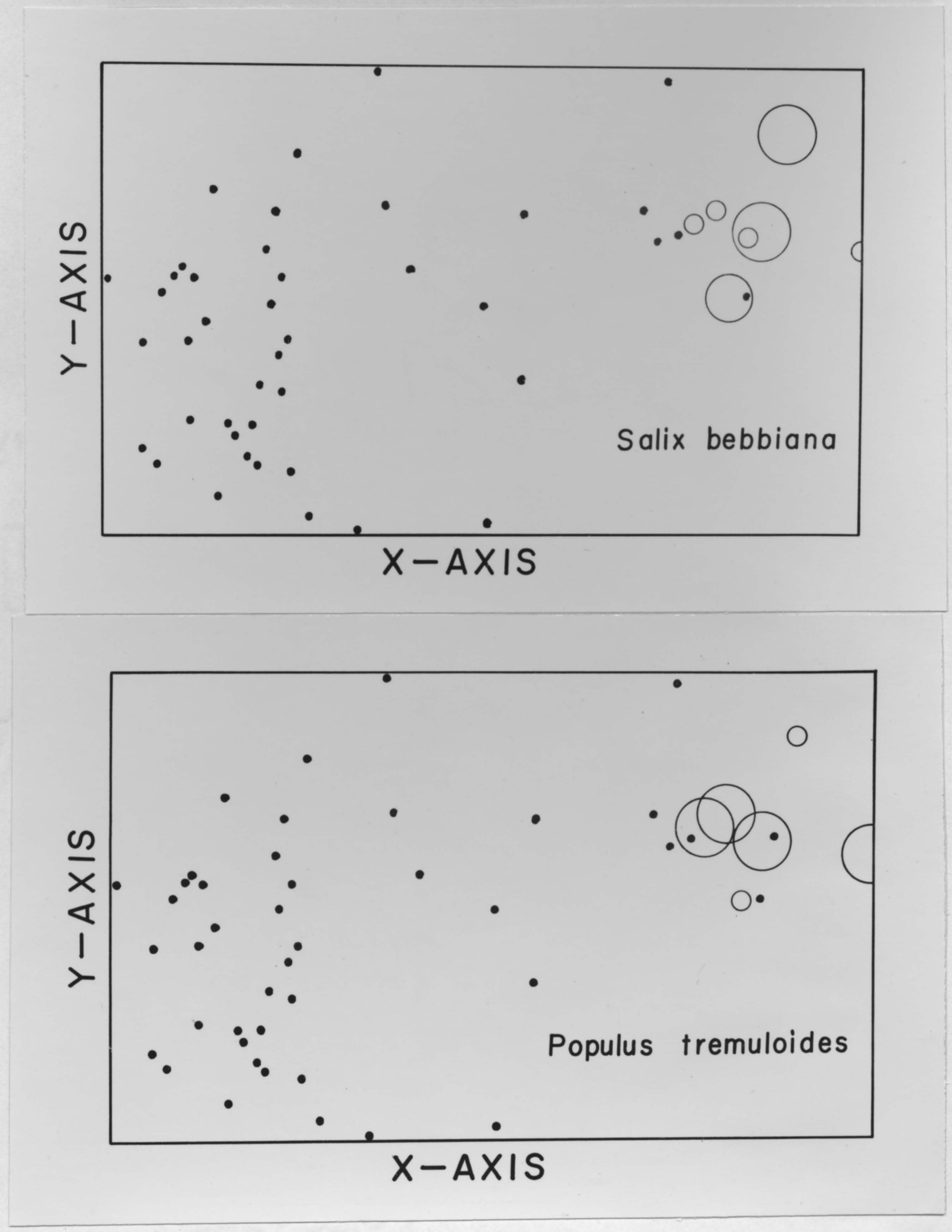


Fig. 28. Phytosociological behavior of two species, which had high frequency towards the right of the X axis (Fig. 22), within the Sceptre X-Y ordination.

Gradients Involved In Distributional Patterns

The species behavioral patterns, represented by the curves and circles, have been used to demonstrate the response of various species to objectively obtained stand orders. Vegetation is affected by many interrelated factorial complexes, although one may be dominant in its effect. Association of distributions with environmental conditions does not imply cause and effect, but may help to discern fundamental relationships between physical and biological phenomena.

Various environmental characteristics may be considered in an attempt to correlate behavioral patterns with habitat. Physiographic, atmospheric and edaphic factors have been found influential in the distributions of plants on dune sand (Cowles 1899; Tolstead 1942; Burzlaff 1960). Species tolerances can also be used to explain what factors are affecting the plants, although exacting physiological and morphological data concerning species involved are often lacking. The following section is an attempt to explain the factors that are affecting the species behavioral patterns in the Dundurn and Sceptre study areas. Edaphic, atmospheric and physiographic conditions in the stand, as well as the morphology of the species have been examined as possible influents on the vegetal patterns.

Dundurn

<u>X</u> - <u>Axis</u>. —— The four physiographic positions in the Dundurn area are aligned along the X axis from left to right as follows: active complexes, stabilized dunes, stabilized blowouts and dune depressions. Table 18 illustrates the correlation coefficients

Table 18. Correlation coefficients between the various measured edaphic properties and also between the edaphic properties and the position of the stand, from which the soil sample was taken, along the X and Y axes in the Dundurn area. Correlations not significant at the 5% level are denoted by an asterisk. OM = organic matter content and WRC = water-retaining capacity.

	% OM	pH	% WRC	% Sand	% Silt	% Clay	X axis position	Y axis position
% OM	-	-.77	+.95	-.85	+.94	+.67	+.64	+.59
pH	-	-	-.74	+.69	-.74	-.54	-.57	-.19*
% WRC	-	-	-	-.95	+.98	+.62	+.68	+.54
% Sand	-	-	-	-	-.99	-.79	-.57	-.72
% Silt	-	-	-	-	-	+.66	+.64	+.58
% Clay	-	-	-	-	-	-	+.16	+.46
X axis position	-	-	-	-	-	-	-	+.07*
Y axis position	-	-	-	-	-	-	-	-

obtained between the X axis position for certain stands and edaphic properties in the same stands. The highest positive correlation is between the X axis and water-retaining capacity, strongly suggesting that the axis is a moisture gradient, ranging from xeric on the left to mesic on the right. The causative agents for such a gradient are undoubtedly complex, but increases in WRC appear due to changes in related edaphic components ($r = +.95$ between OM and WRC and $r = +.98$ between silt and WRC). The WRC also reflects the percentage sand present, since a correlation of -.95 occurred between sand content and WRC. The high sand percentage in stands occurring to the left of the axis results in more xeric conditions, particularly in surface layers where the low specific heat of the sand particles allows rapid warming and high moisture evaporation. The relatively large sand particles also have a small surface area and thus retain little water. Richardson (1920) and Duke (1960) have reported that sand dunes are very porous, well drained and have extensive lateral movement of water, factors which result in a xeric habitat for the growth of plants.

Stands occurring towards the right extreme of the axis have higher silt percentage, possibly because of washing of such particles down from surrounding dunes into the depressional stands as reported by Wells and Shunk (1931), which results in a large surface area and a high WRC. The differences in available soil moisture between active complexes and dune depressions are demonstrated in Table 19. It is evident that active complexes are low in moisture content in the surface layers, but have increased moisture at depths below six inches. In dune depressions, however, the moisture content in the top six inches is approximately six times that in surface layers

Table 19. Total moisture percentage on the four physiographic positions in the Dundurn area. Data based on nine samples throughout growing season. AC = active complex, SB = stabilized blowout, SD = stabilized dune and DD = dune depressions.

Depth	Physiographic position			
	AC	SB	SD	DD
0"-6"	1.64	2.61	4.58	9.25
6"-36"	3.20	1.67	2.74	5.58

in active areas. Even below six inches in dune depressions, the moisture percentage is greater than for any other position.

The negative correlation between pH and the X axis is possibly a function of the greater moisture and organic conditions in the depressions, since leaching of bases and addition of humic acids in depressional areas would be expected to increase the hydrogen-ion concentration. Table 20 illustrates the variation in pH between the four physiographic positions in the Dundurn area. Active complexes are slightly alkaline, stable blowouts and dunes are near the neutral point and dune depressions are acidic. Similar variations in pH due to physiography have been reported in England by Salisbury (1952), Webley et al. (1952) and Ranwell (1959). The variation in pH is related to a change in $CaCO_3$ content (Table 14), since active complexes are highest in $CaCO_3$, followed in rank by stable blowouts, stable dunes and finally dune depressions.

Variations in organic matter content also occurred along the X axis (Table 20). Active complexes are lowest in organic matter, followed by, in increasing order, stable blowouts, stable dunes and dune depressions, in which the organic matter content reaches the measured maximum. Even in the depressions, however, the organic content is relatively low when compared to finer textured soils. The diversity in the organic content is reflected by the variation of the surface layer colors. Active complexes are greyish-brown in color to a depth of 42 inches; deeper samples are brown. Dune depressions are, in contrast, dark-greyish brown to a depth of 36 inches.

Atmospheric conditions on the physiographic positions also support the conclusion that the X axis approximates a moisture gradient.

Table 20. Soil characteristic values for five stands in each of the four physiographic positions in the Dundurn area. * denotes only two depths analyzed. ≠ denotes modal value.

Physiographic position	Color≠	pH≠	% WRC	% OM	% Sand*	% Silt*	% Clay*	$CaCO_3$ rating
Active complexes								
0"-4"	5/2	8.2	11.3	0.4	92	1	7	3
4"-12"	5/3	8.2	11.4	0.5	-	-	-	4
12"-36"	5/3	8.2	11.5	0.6	-	-	-	4
Stabilized blowouts								
0"-4"	4/2	7.2	15.0	1.3	83	10	7	1
4"-12"	5/3	7.5	12.7	0.9	-	-	-	1
12"-36"	5/4	7.6	11.6	0.7	-	-	-	3
Stabilized dunes								
0"-4"	4/2	7.1	18.2	2.3	70	20	10	0
4"-12"	4/3	7.3	14.8	1.2	-	-	-	1
12"-36"	5/4	7.2	12.6	0.8	-	-	-	3
Dune depressions								
0"-4"	4/2	5.8	20.7	3.0	58	27	15	0
4"-12"	4/2	5.9	16.4	2.2	-	-	-	0
12"-36"	4/2	6.0	15.1	0.8	-	-	-	0

The atmosphere on active complexes is xeric, particularly on windward dune slopes (Cowles 1899; Whitfield 1932; Ramaley 1939; Tolstead 1942; Laing 1958; Olson 1958). Wind velocities, insolation and evaporation are also high on active sand areas (Gleason 1910; Park 1931). Rempel (1937) lists two major reasons for the inability of plants to colonize moving barchan dunes, lack of moisture and a rapidly shifting surface. Depressional areas, however, usually have a less xeric atmosphere, due to reduced wind velocities (Tolstead 1942).

Total moisture determinations (Table 19) indicate that stable blowouts are more xeric than stable dunes, particularly in surface layers. With this the situation, it is unusual that stable dunes stands occur to the left of those on stabilized blowouts along the X axis, in what would appear to be the reverse order, if the axis is a moisture gradient. An inspection of species involved and consideration of the secondary axis reveals information concerning the apparent anomaly in stand distribution.

Y - Axis. —— It should be remembered that constructed axes represent compositional gradients assumed to be in response to environmental gradients affecting the plants and that interrelations of factors may prevent assignment of one factor as predominant in influencing the vegetation. The unusual stand order on the moisture gradient seems explainable on the basis of the distribution of the physiographic positions on the X-Y coordinates and knowledge of the relative stability of the habitats and their specific components. From the X axis alone, it was impossible to tell if the stands were actually located in the same plane. Construction of a secondary axis and subsequent plotting of physiographic positions in two dimensions illustrated that certain stands along the X axis were actually separated when plotted in two dimensions (Fig. 15).

The stand positions along the two axes in the Dundurn area were not correlated (Table 18), indicating that construction of the Y axis yielded a new compositional gradient representing a different environmental complex. A positive r value of 1.00 would have indicated that the position of the stands on each axis was the same, making unnecessary the use of the Y axis in further study of species distributional patterns.

Stabilized dunes occur above 48 on the Y axis (Fig. 15), while active complexes, stable blowouts and dune depressions remain closely associated to the X axis. The Y axis reflects stabilization of active complexes, which would explain increases in WRC as organic matter was added to the soil upon stabilization and would agree with observations concerning active complexes succeeding into stable dunes.

The unstable xeric conditions on active complexes are exemplified by the rhizomatous habit (Psoralea lanceolata, Agropyron spp. and Calamovilfa longifolia) and deeply penetrating roots (Lygodesmia juncea, Calamovilfa longifolia, Psoralea lanceolata) present in important species on such positions. These characteristics allow growth on dry shifting surface layers (Gleason 1910) and utilization of moisture at lower levels (Table 19) (Starr 1912; Willis et al. 1959). Annuals found on active dunes, such as Corispermum orientale, also have an advantage on active complexes due to their short life cycle in favorable periods, particularly spring (Rempel 1937). Lack of competition by other species is also a probable factor affecting the growth of both annuals and perennials on bare sand.

Considerable work has been done on the microbiology of the zone around underground organs of plants adapted for growth on bare sand. Webley *et al.* (1952) traced the development of microflora from bare sand to more stabilized areas and found that a marked variation of fungal populations occurred along with the vascular flora changes. He also found that root systems of dominant colonizing species on xeric dunes had a particular rhizosphere flora. Similar findings have been reported by Brown (1958) and Salisbury (1952). It is probable that such microbiologic relationships exist on Saskatchewan dunes, although no investigations of this nature have been made.

Dune stabilization results in the prevalence of more shallowly rooted species (*Stipa comata*, *Carex eleocharis*, *Artemisia frigida* and *Selaginella densa*), which presumably can more efficiently utilize moisture in surface layers (Table 19) of the dunes. The absence of adaptatory characters, such as rhizomes, which hindered their growth in erosional and depositional areas, is not detrimental in this more stable habitat. These species reach peak frequencies in the upper middle of the X-Y ordination (Figs. 18 and 19). In contrast, species distributed in the lower right on the X-Y coordinates (Figs. 20 and 21) appear to be definitely related to a moisture gradient. On stable dunes the elevation above the water table is great, possibly resulting in more xeric conditions than on stabilized blowouts or dune depressions.

The occurrence of *Juniperus horizontalis* in stable blowouts is correlated in part to its adaptation to the erosive and depositive environment. The radial mat of growth prevents erosion and the upturned branch tips can withstand limited deposition (Olson 1958). Thus, while herbaceous species are colonizing the blowout bottom, this prostrate shrub often establishes circular clones (Cosby 1960) on the edges and finally by extensive branch propagation covers the blowout completely (Van Denack 1961).

The presence of Juniperus affects the herbaceous composition on stable blowouts, as illustrated by the negative correlation between Juniperus cover and forb density.

Van Denack (1961) reported that shading by Juniperus horizontalis on stabilized blowouts near Lake Michigan was responsible for controlling grass and forb growth. The presence of Juniperus probably affects the moisture status in stable blowouts, since species found in moist dune depressions also grow in stable blowouts. Carex heliophila, for example, attains high frequencies in stable blowout stands and in dune depressions. Other species, whose ecological optimum is usually centered in areas of favorable moisture, occurring within the Juniperus mat include: Solidago missouriensis, Festuca ovina, Festuca scabrella and Galium borale. Van Denack (1961) reported similar observations with Galium borale. The similar floristic composition of stands occurring in stable blowouts and dune depressions is apparent from the low interstand distance separating these sites on the X-Y graph.

Water table depth is another possible factor affecting species distributions in blowouts and depressions (Tolstead 1942; Russell and Rhoades 1956; Ranwell 1958). Ranwell (1959), however, concluded that the water table is usually not a significant influence on vegetation when deeper than one meter below the soil surface. In the Dundurn area, where the water table is approximately three to seven meters below the surface in depressional areas (Mackay and Maddox 1936), it seems that this factor would be eliminated. Gimingham (1955) found, however, that the boundary of an oasis in the North African desert and the proximity of the water table were correlated, even when the water table depth was approximately 20 feet.

Dune depressions may receive additional moisture from water percolating downward and then laterally into depressions from surrounding dunes (Salisbury 1952; Ranwell 1959). The higher silt and clay content in dune depressions would prevent loss of precipitation due to rapid percolation to the water table. Ranwell (1959) found that soil development occurred more rapidly in depressions, because of high organic matter content. The origin of the organic matter was from shrubs and graminoids growing in such locations.

Sceptre

X - Axis. —— The primary axis in the Sceptre area is also positively correlated with WRC (Table 21). Organic matter ($r = +.93$ between WRC and OM), silt ($r = +.63$ between WRC and silt) and clay ($r = +.94$ between WRC and clay) apparently are responsible for the improved WRC along the X axis. There is a negative correlation between the percentage sand content and the primary axis, as was found in the Dundurn area. The correlation between WRC and the X axis in this study area is stronger than in the Dundurn area. There, however, is no correlation between the X axis and pH in the Sceptre area. This may be due to less leaching of bases to a non-returnable depth.

Table 22 illustrates the various soil characteristics analyzed

Table 21. Correlation coefficients between the various measured edaphic properties and also between the edaphic properties and the position of the stand, from which the soil sample was taken, along the X and Y axes in the Sceptre area. Correlations not significant at the 5% level are denoted by an asterisk. OM = organic matter content and WRC = water-retaining capacity.

	% OM	pH	% WRC	% Sand	% Silt	% Clay	X axis position	Y axis position
% OM	-	-.29*	+.93	-.56	+.66	+.88	+.66	+.66
pH	-	-	-.23*	+.20*	-.02*	-.02*	-.07*	-.20*
% WRC	-	-	-	-.84	+.63	+.94	+.98	+.14*
% Sand	-	-	-	-	-.80	-.67	-.55	-.38
% Silt	-	-	-	-	-	+.60	+.51	+.25*
% Clay	-	-	-	-	-	-	+.58	+.57
X axis position	-	-	-	-	-	-	-	+.47
Y axis position	-	-	-	-	-	-	-	-

Table 22. Average soil characteristic values for five stands in each of the three physiographic positions in the Sceptre area. * denotes only two depths analyzed. ≠ denotes modal values.

Physiographic position	Color≠	pH≠	% WRC	% OM	% Sand*	% Silt*	% Clay*	$CaCO_3$ rating
Active complexes								
0"-4"	6/4	8.2	12.0	0.5	93	3	5	1
4"-12"	6/4	8.3	11.6	0.5	-	-	-	3
12"-36"	6/4	8.3	11.4	0.3	-	-	-	4
Stabilized dunes								
0"-4"	6/4	7.9	13.6	0.8	87	6	7	1
4"-12"	6/3	8.1	12.7	0.6	-	-	-	2
12"-36"	6/3	8.0	12.3	0.5	-	-	-	2
Sand flats								
0"-4"	5/2	7.5	15.6	1.4	71	18	11	0
4"-12"	6/4	7.7	15.4	1.4	-	-	-	3
12"-36"	6/4	7.9	18.6	1.5	-	-	-	4

for stands in the Sceptre area. The variations in the soil properties appear related to physiography. Active complexes are alkaline in reaction to a depth of 36 inches, presumably due to the presence of calcium carbonate. Organic matter content is low in active areas, because of lack of mulch deposition by the vegetation and rapid oxidation in the coarse porous sand (Cowles 1899; Hepburn 1952). Silt and clay percentages are also low in active complexes, with 93% of the textural distribution in the sand fraction. The high sand and low organic content results in low water-retaining capacities. Atmospheric conditions are also xeric on active areas.

Edaphic conditions on stable dunes and active complexes differ in that surface pH is lower and organic matter, silt and clay content is higher on the stabilized dunes resulting in a somewhat greater WRC in such areas. This, and the increased stability of the sand surface is reflected by the vegetational composition. Species lacking extensive rhizome development or deeply penetrating root systems are more frequent on stable dunes, whereas species possessing these adaptations are more common on active complexes. Surface dryness and instability appear to be the factors governing distributional patterns on active complexes. Stable dunes, possessing higher organic content and WRC, support species that are more shallowly rooted and less adapted to sand erosion.

Edaphic conditions on the third physiographic position in the Sceptre area, the sand flats, are more mesic than either active complexes or stable dunes. Because of greater organic matter, silt and clay content, the WRC of the soil is higher. The pH is still above neutral, but less alkaline than on active complexes. The soil is darker in color in surface layers. This is presumably due to higher quantities of organic matter. Similar increases in organic matter content and water-retaining capacity and decreases in pH upon dune stabilization were reported by Billings (1938). Calcium carbonate was not detectable in surface layers of the flats (Table 22). This is probably due to leaching. It has been reported that $CaCO_3$ and pH are often low in soil profiles in mesic areas, while organic carbon is high (Kurz 1923; Hepburn 1952; Burges and Droves 1953; Gorham 1958).

It was observed that a layer of compact soil occurred in the flats at a depth of approximately 12 inches. An analysis of this layer demonstrated that it was mainly silt and clay. Although the layer was present to a depth of at least 36 inches on the flats, it was not present on active complexes or stable dunes. It is conceivable that in the initial deposition of the materials in this area, a layer of fine-textured particles was deposited in a glacial lake bottom, probably the same lake that gave rise to the heavy clay deposits of the Sceptre area. This would explain the level nature of the sand flats and the apparent superimposition of the dunes upon the flats. The water table is near the surface in the level areas, from five to fifty feet, and may originate from surface water percolating downward through porous dunes (Mackay *et al*. 1936).

Although presence of the water table near the soil surface may account for the occurrence of shrubs and trees on sand flats, other factors affect the vegetational composition. The herbaceous vegetation of the sand flats is affected by increased WRC of surface layers. An additional factor is the presence of a mat of *Juniperus horizontalis*, reducing evaporation and increasing the moisture status of the flats. Stable physiographic conditions on the flats probably result from nearness of the water table to the surface, combined with the protection afforded by the *Juniperus* canopy.

The mesic nature of the sand flats is exemplified by the presence of shrubs and trees in an area surrounded by grassland vegetation. There is only limited extension of the woody species onto stable dunes. *Artemisia cana* is the most conspicuous of these woody plants, but *Prunus virginiana* and *Rosa woodsii* are often present. Isolated individuals of *Populus deltoides* var. *occidentalis* often occur on the dunes, but these seem the result of burial and elongation processes involving lee slopes of active dunes. *Salix interior* was observed growing near the base of dunes and it is suspected that such plants are rooted in the moist substrate of the sand flats. Bruner (1931) found such to be the situation in Oklahoma dunes with *Salix* and *Populus*. These genera apparently survive burial, through their ability to elongate more rapidly than the sand is deposited. Cowles (1901, 1911) reported that *Salix glaucophylla* and *S. syrticola* (*S. adenophylla*) were able to adapt themselves to burial by vertical elongation and production of roots from buried stems. Similar growth patterns were described by Ranwell (1960) for *Salix repens*.

In most cases, an increase in elevation above the sand flat resulted in a sharp decrease in the presence of *Juniperus horizontalis*, along with other shrubs and trees. This was particularly obvious around the dune base. In such locations, the shrubs were able to establish themselves a short distance up the slope of the dune, but additional increase in elevation above the sand flat were accompanied by reduction in shrub densities and increases in grasses and forbs characteristic of stable dunes.

Y - Axis. — Correlations between the Y axis and edaphic properties in the Great Sand Hills showed that, although organic matter increased with stabilization, there was not a significant correlation between WRC and the Y axis. This suggests that changes in moisture status on the Y axis may be less important than changes in some other factor. This is different than in the Dundurn area, where the Y axis was correlated with WRC, although not as strongly as the X axis. It is possible that the moisture factor is so predominant in its effect on the vegetation that changes due to other gradients are hidden. Figure 29 and Table 21 indicate that the stand order is similar whether viewed from the X or Y axis. The Y axis does not, however, separate active complexes from stable dunes as well as does the X axis. If the Y axis is a stability gradient, this is not surprising, since it was observed that stabilized dunes and active complexes were more similar floristically in the Sceptre area than in the Dundurn area. A marked separation of active complexes and stabilized dunes occurred in the latter area. The location of those stands occurring on sand flats, in the upper portion of the Y axis and towards the right on the X axis, is evidence that the X and Y axes represent moisture and stability gradients, respectively. These stands were observed to be the most mesic in the area and also the most stable, physiographically.

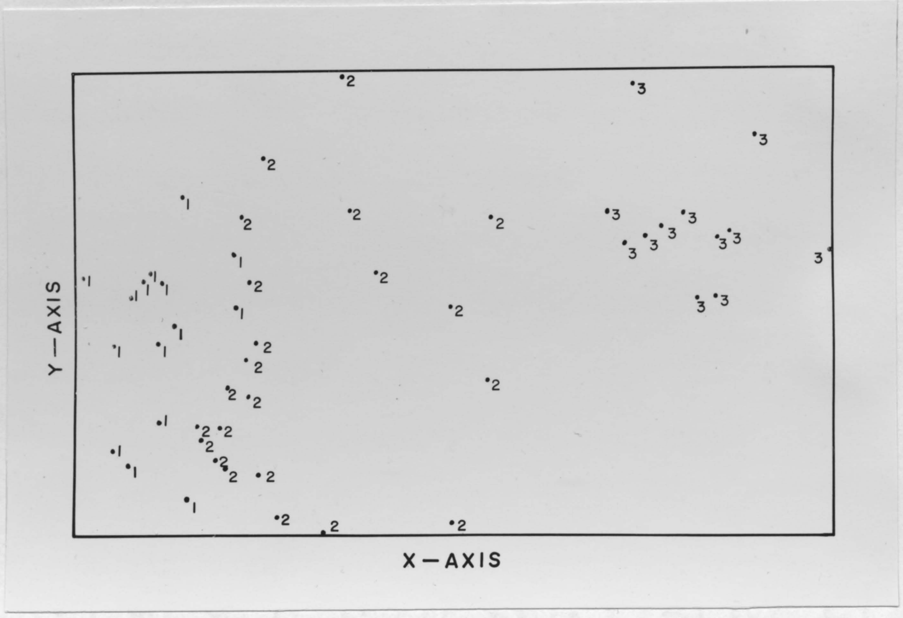


Fig. 29. The distribution of stands within the Sceptre ordination according to physiographic position. 1 = active complexes, 2 = stabilized dunes and 3 = sand flats.

DISCUSSION

This study is an attempt to examine the distributional patterns of species occurring on two dune sand areas in the grassland region of Saskatchewan. Two main presentations of data are made. The first consists of establishing physiographic categories, with reference to stability, and averaging various quantitative values representing the success of the species within these categories. The results of this presentation indicate that most species reach their optimum in only one physiographic habitat, although some species exhibit bimodal tendencies. Most of the species distributions resembled normal curves, possessing minimal, maximal and optimal points.

The second analysis was based entirely on the floristic composition of the stands. No reference was made to the habitat in which the stands were located. Quantitative data for component species were used to determine the spatial arrangement of the stands in one and two dimensional ordinations. When the behavioral patterns of selected species along the ordination were examined, it was found that they were similar to those presented for the physiographic gradient. The species critically examined tended to occupy a specific portion of the linear gradient or possessed distinct centers of action within the two dimensional presentations.

The patterns established by the two analytical treatments appear to be a reflection of the adaptive characteristics possessed by the plants. These characteristics allow utilization or tolerance of environmental gradients presented by the particular habitat in which the plant attains its optimum success. The following section will consider firstly, the factors involved in the vegetal patterns in the Dundurn area, followed by a consideration of those in the Sceptre area and lastly, by general conclusions concerning the nature of the entire dune vegetational complex.

Dundurn Area. — Actively blowing complexes originate from stabilized dunes. This occurs through a cyclic pattern involving stabilized dunes and conditions resulting in the death or reduction of the vegetative cover on such areas. Reduction of the vegetative cover is likely to promote the formation of new blowout-dune complexes. The dune portion of the complex is subsequently stabilized by vegetation, completing the cycle.

The actively blowing areas present a severe environment for the growth of most plants, which results in a sparseness of vegetation and perpetual erosion and deposition. The ability of plants to survive on active complexes is primarily related to deeply penetrating roots and extensive rhizomes, morphological features that secure moisture from the sub-surface levels and also prevent substrate erosion. As long as erosion and deposition continue, most plants are unable to inhabit such areas, but with decreases in either of the processes, invasion of blowouts and dunes by less adapted taxa increases markedly. Cessation of erosion may result from depletion of sand supply or from any factor causing reduction of the ability of the wind to move the sand.

Development of a vegetative cover on active complexes has two courses, one on the blowout portion of the complex and one on the dune portion. Both are governed by the physical environment of the particular habitat. Reduction of erosion from the bottom of blowouts is accompanied by an increase in the density of herbaceous species. Along with the herbs, there occur a few small patches of *Juniperus horizontalis*, the growth habit of which is well suited to the still unstable habitat. *Juniperus* is tolerant of the effects of wind during early phases of blowout stabilization and has deeply penetrating roots reaching to the capillary fringe of the water table, which, in the depressional blowouts, is relatively near the surface. This prostrate shrub, which often has as an associate, *Arctostaphylos uva-ursi*, apparently restricts herbaceous growth, favors reproduction of woody species under its branch canopy as suggested by Olson (1958) and has a distinct effect on the microenvironment of the blowout habitat in the form of shading (Van Denack 1961). Shading presumably reduces evaporation, which in turn affects moisture conditions under the shrub canopy. One result is that the herbaceous flora in blowouts is composed of species characteristic of areas having high moisture content.

Beyond the *Juniperus* stage, the path of vegetational development in blowouts is not clear. Since shrubs, such as *Elaeagnus commutata* and *Rosa woodsii*, are favored by the microenvironment of the blowout while small and are able to root in the moist subsoil at maturity, it is possible that the blowouts will become increasingly dominated by these shrubs, to which *Prunus virginiana* and *Amelanchier alnifolia* may be added in the future. The next logical step in a linear successional series would have aspen groves forming in the blowouts. Maini (1960), however, concluded that groves in the grassland region of Saskatchewan are relicts of a previously more extensive coverage of the area by boreal-deciduous forest and that it is unlikely that aspen is spreading into favorable areas such as sand dune blowouts and forming young groves. He found no evidence of sexual reproduction of the species and contended that the only invasion into grassland by aspen is by asexual means in areas immediately surrounding the present groves.

The counterpart of the blowout, the active dune, presents an even more severe habitat for plant growth, although colonizing species included adapted forbs and grasses similar to the blowout colonizers. The severity of the habitat results from the xeric nature of the dunes, which cause a high susceptibility to erosion upon reduction of the vegetative cover. The vegetation occurring in stabilized dunes differs considerably from that in stabilized blowouts. The constituents of the vegetation on stabilized dunes are principally shallowly-rooted species not possessing the adaptatory faculty of rhizomatous growth, but having the advantage of shallow roots, which allow utilization of moisture present in the surface layers of the sand. Dunes also present a less satisfactory habitat for the growth of deeply-rooted species, since the water table is further below the sand surface than in blowouts.

The vegetation developed through stabilization of active dunes is a grassland dominated by Stipa comata, Koeleria cristata, Carex eleocharis and Artemisia frigida. Such stabilization is the result of reactions between the vegetation and the habitat presented by the original dune. The species compositional gradient ranging from actively eroding complexes to stabilized dune grassland represents succession. Such reaction progressively modifies the environment of the dune to a degree where the less adapted grassland species can inhabit the area.

In contrast, the vegetation in dune depressions is the product of an unknown successional development on the physical characteristics offered by such areas. These include high water-retaining capacity, organic matter content and silt and clay fraction. That such areas are mesic is evidenced by the presence of shrubs and trees in an otherwise grassland region. The vegetation in dune depressions is probably changing less rapidly than that on active complexes, reflecting a stable state, which is governed in its development by factors peculiar to this physiographic position. It is doubtful if the depressions are ever directly reactivated into actively blowing areas, since moisture conditions in such locations are not conducive to erosion. It is probable, however, that a long-range view would see the depressions being filled with sand from an adjacent moving dune, thus destroying the mesic vegetation that is presently occupying the habitat. Barring such, the depressions will presumably become increasingly dominated by shrubs, much in the same manner as the blowouts.

Sceptre Area. —— Although the above discussion pertains particularly to the Dundurn area, the situation in the Sceptre area is much the same. Species composition and factors operative on active complexes are similar to those in the Dundurn area and stabilization of moving sand results in the growth of species that are shallowly rooted and less adapted to erosion and deposition.

The vegetational gradient ranging from active complexes to stabilized dunes is the result of succession on the dune habitat. This, as in the case of the Dundurn area, is in contrast to patterns existing in the vegetation due to variations in habitat. Such a habitat gradient exists in the Sceptre area, from xeric active complexes (low in organic matter and fine soil particles and being a great distance from the water table) to the mesic sand flats (having greater amounts of organic matter, fine soil particles and a closer proximity to the water table).

Vegetational Complex. — It seems likely, therefore, that vegetal patterns existing in the two study areas result from the interaction of two gradients, succession and moisture. The first gradient, succession, has evoked many theories as to possible causes, courses and outcomes. Most successional studies attempt to align differing vegetational units along a temporal axis, because to observe a given area over a long enough period to determine the cause of succession is almost impossible. Therefore, the obvious recourse is to study spatially separated areas and place these in a logical temporal sequence. Such sequences are often synthetic and mask unanswered questions concerning factorial gradients, other than time, which are affecting patterns in the vegetation. Because of this, rather than suggesting an idealized successional scheme, it is proposed that patterns in the dune sand vegetation in Saskatchewan result from autogenic succession (Tansley 1935), taking place under the influence of a particular set of variables, which include time, substrate and physiography.

The remaining patterns in the vegetation are due to the complex environmental gradients that are related to continuously varying habitats. The major habitat gradient is moisture. This gradient is controlled by physiography, which affects both edaphic and atmospheric moisture status. The moisture and stability gradients in turn affect the vegetation, which responds in a continuous fashion as evidenced by the species behavioral curves. There exist, of course, sharp breaks in continuity, but these appear due mainly to abrupt changes in the environment, similar to the telescoping of successional stages or "cornering" as described by Dansereau (1957). The results of this study substantiate the suggestions of Whittaker (1953), Curtis (1955), Olson (1958) and others, which consider that vegetation is governed in its development and distribution by continuously varying habitat gradients.

Whether a continuum exists between the vegetation on fine-textured soils and dune sand deposits is not certain. It may be possible in the future to establish whether this is the situation, by quantitatively sampling grassland and forest stands on finer-textured soils (Coupland 1950, 1961). These data could then be used to establish compositional or environmental gradients, study species behavior and to possibly assign various environmental conditions as influents on the vegetation.

SUMMARY

The purpose of this investigation was to ascertain species distributional patterns on dune sand areas located in the grassland region of Saskatchewan and to attempt to relate these distributions to factors present in the environment of the vegetation. Two study areas, one near Dundurn and the other in the Great Sand Hills, were selected for use in the study.

A total of 101 stands located on various physiographic positions were sampled by one-quarter m^2 quadrats, yielding data on the absolute frequency of species. The point-centered quarter method was used in 63 stands to obtain relative frequency, relative density, absolute density and importance values for the principal species. Additional sampling was done in some stands using the point-transect frame and the line and belt transect. Soil samples were taken in many stands and analyzed quantitatively for organic matter content, pH, water-retaining capacity and texture and qualitatively for color and calcium carbonate.

Two approaches were utilized in the analysis and interpretation of data obtained from the sampling of the vegetation and soils. The first involved the presentation of the vegetative composition with reference to the physiographic positions on which the stands were located. This analysis indicated that the phytosociological behavior of most species approximated a normal distribution and represented the ecological tolerance of the species to factors present in the environment of the vegetation. It was found that most species reached a peak in importance in only one physiographic position, although some

did exhibit bimodal tendencies. Because of this, patterns resulting from more than one environmental gradient were sought.

The second analytical technique was entirely phytosociological in that quantitative values for the species were used in aligning the stands in a spatial order indicative of their similarity. Such an ordination technique allows the resolution of more than one gradient in the environment of the vegetation. Primary and secondary ordinations were constructed by the use of similarity coefficients.

Absolute frequency values for selected species were then plotted on the primary ordination and in relation to the primary and secondary ordination axes. Species behavioral curves formed in relation to the primary axis resembled normal curves or portions of such curves. Some species, however, exhibited curves that appear to be bimodal, a situation similar to that found in the analysis of the data with respect to the physiographic categories. The bimodal tendencies were found to be the result of more than one gradient operating in the environment or in some instances the result of difficulties in differentiating the specific members of a genus. The behavioral curves on the X-Y coordinates can be described as spheres of activity, achieving a maximum in a particular portion of the environment and decreasing in value towards the periphery of the optimum location.

Actively blowing complexes had as principal species, Psoralea lanceolata, Oryzopsis hymenoides, Helianthus petiolaris and Lygodesmia juncea. Stabilized dunes supported grassland dominated by Stipa comata, Koeleria cristata and Artemisia frigida. Habitats that were depressional or that possessed other physical conditions resulting in a mesic environment supported the growth of shrubs and trees

(*Juniperus horizontalis*, *Symphoricarpos occidentalis*, *Rosa woodsii*, *Populus tremuloides*, *Salix bebbiana*), along with herbs such as *Carex heliophila* and *Solidago missouriensis*.

Factorial gradients involved in the distributional patterns include a moisture gradient, ranging from xeric to mesic habitats and autogenic succession, from active complexes to stabilized areas. The existence of the gradients and the intergradation of the behavioral patterns of the principal species along the gradients offer strong evidence for the continuous nature of the vegetation on dune sand in Saskatchewan and suggests that the "climax pattern" concept is the most adequate means for describing the vegetation.

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APPENDIX A

Scientific and common names for major species in Dundurn and Sceptre area.

Scientific Name	Common Name
Agropyron spp.	wheat grass
Arctostaphylos uva-ursi	bearberry
Artemisia campestris	plains wormwood
Artemisia cana	hoary sage-brush
Artemisia frigida	pasture sage
Artemisia ludoviciana	prairie sagewort
Betula occidentalis	river birch
Bouteloua gracilis	blue grama
Calamovilfa longifolia	sand grass
Campanula rotundifolia	hare-bell
Carex eleocharis	low sedge
Carex heliophila	sun-loving sedge
Chrysopsis villosa	hairy gold aster
Corispermum orientale	bug-seed
Elaeagnus commutata	wolf willow
Elymus canadensis	nodding wild rye
Festuca ovina	sheep fescue
Helianthus petiolaris	prairie sunflower
Juniperus horizontalis	creeping juniper
Koeleria cristata	june grass
Lygodesmia juncea	skeleton weed
Oryzopsis hymenoides	indian rice-grass
Phlox hoodii	moss phlox
Populus balsamifera	balsam poplar
Populus tremuloides	aspen
Prunus virginiana	chokecherry
Psoralea lanceolata	lance-leaved psoralea
Rosa woodsii	Wood's rose
Rumex venosus	sand dock
Salix bebbiana	beaked willow
Salix interior	sandbar willow
Selaginella densa	prairie selaginella
Solidago missouriensis	low golden-rod
Sporobolus cryptandrus	sand dropseed
Stipa comata	spear grass
Symphoricarpos occidentalis	western snowberry