

VEGETATIVE COLONIZATION AND SUCCESSION  
AND THE IMPACTS OF TRAMPLING IN  
THE CARBERRY SAND HILLS, MANITOBA

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Submitted to  
The Faculty of Graduate Studies  
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by  
Marjorie Herring Ward  
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## ABSTRACT

The Carberry Sand Hills of Manitoba, an area of bare and stabilized dunes and rolling prairie are described in terms of their environmental characteristics and plant communities. Four successional stages were examined between May and October in 1976 and 1977. Data indicate that open dunes move 15 to 20 cm a year and have scattered areas colonized by Andropogon gerardi, Oryzopsis hymenoides and Helianthus petiolaris. Complete colonization of the dunes is expected between 1987 and 1994. Sites intermediate between bare dunes and prairie are vegetated by Andropogon gerardi, Koeleria cristata, Elaeagnus commutata, Petalostemum candidum, Andropogon scoparius and Bouteloua curtipendula. Prairie species include Juniperus horizontalis, Stipa spartea, Carex spp. and Bouteloua gracilis.

Species behavior follows two patterns: either a maximum prominence (cover  $\sqrt{\text{frequency}}$ ) is attained at the time of flowering or two maxima are attained corresponding with the times of flowering and vegetative reproduction respectively.

Increasing vegetation development is accompanied by a decline in pH and an increase in organic matter. Nutrient levels in all soils are low and probably limit growth.

Ordination of community replicates shows nitrogen, organic matter, conductivity and pH to be controlling factors in community distribution. In the two years of the study, rainfall was a deciding factor in community composition and species behavior.

A study of trampling impacts on the four communities showed that all sites were damaged by 20 bi-weekly tramples. Species which were able to recover included Petalostemum candidum, which reproduced by seed on Site II, and Andropogon gerardi, which reproduced from rhizomes on Site III. Mosses and Artemisia frigida were observed in the recovery phase in the prairie trample plots.

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## INTRODUCTION

The Carberry Sand Hills of Manitoba are unique in both their beauty and plant communities, and it was these two aspects which prompted research in the Sand Hills. Open dunes, with white, blowing sand proceed through several changes in their plant communities to become rolling prairie, with groves of aspen and scattered white spruce. Thus, the first aspect of this research was to study the colonization and succession on the Sand Hills.

To date, relatively little is known about the plant communities and environmental factors of the Carberry Sand Hills. Chronological studies of the area showed five major periods of dune activity associated with drought that began after 3700, 2100, 1500, 900 and 400 years B.P. (David, 1971). Bird (1927, 1961) discussed dune movement, summarized climatic records between 1887 and 1924 and gave a brief discussion of plant species found in the dunes and associated sand prairie. Criddle (1927) published a list of plants for the area with their dates of flowering and seed ripening. A publication on the distribution of mammals in the sand hills of southwestern Manitoba in relation to plant communities briefly described vegetation in the Carberry Sand Hills (Wrigley, 1974). Popular articles on the Carberry Sand Hills were written by Nero (1971) and Dubois (1976).

The first objective of the present study was to add to our meager knowledge of plant colonisation and succession in the Carberry Sand Hills. Because the unique beauty of the area is drawing more visitors every year, the second aspect of this study was to determine how sensitive the Sand Hill communities are to trampling pressures. In spite of the fact that a number of trampling studies have been undertaken in a variety of ecosystems, and their results are strikingly similar, there are many problems in the design and execution of such experiments. This study allowed an opportunity to assess the objectives and methodologies of one facet of applied ecology.

CHAPTER 1  
LITERATURE REVIEW

A review of some of the pertinent literature is presented in two sections. The first gives information about dune and prairie colonization and succession, and the second discusses trampling impacts on natural ecosystems.

#### COLONISATION AND SUCCESSION

Sand and Dune Movement. Dunes are found world wide where there are large accumulations of sand in deserts, on sea coasts or lake shores and inland deposits from glacial lake deltas. All dunes are formed by the action of the wind on loose unconsolidated sand. Dune shape is determined by vegetation, wind speed and direction, and sand supply. Bagnold (1941) discussed the physics of sand movement and development of desert dunes where the effects of vegetation are minimal or non-existent. Bagnold's primary emphasis was on particle sizes, the wind speed required to move various sizes, and wind flow patterns associated with different dune forms.

Inland and coastal dunes have different forms from desert dunes due to the vegetation which interferes with wind speed and direction, and to the amount of sand available. Hack (1941) considered transitions between transverse, parabolic and longitudinal forms found in the southwestern United States. Dunes in Alberta were discussed by Odymsky (1958) who also observed various forms and found the effectiveness of winds in shaping dunes depended upon the dryness of the ground and wind velocity. Strong winds for a short duration were more

effective in moving sand, and therefore affecting dune shapes, than mild sustained winds.

Ecologists have been interested in the interrelationships of vegetation and dune formation since Cowles' (1899) reported on the dunes of Lake Michigan. Later workers described the effects of vegetation and topographic form of dunes on the processes of erosion in blowouts and subsequent stabilization. Olson (1958b) noted that the parabolic shape of dunes crowded and accelerated wind at dune crests, creating wind erosion and new blowouts on the most exposed part of the dune. Dune orientation in relation to wind and vegetation in Britain and Denmark was discussed by Landsberg (1956) and on inland dunes in Idaho by Chadwick and Dalke (1965). The growth of dunes caused by vegetation arresting wind and sand movement, followed by dune breakdown by slope wash and creeping was described by Smith (1934) for Kansas dunes.

Environmental Factors. The ability of plants to colonize new areas is dependent to a large degree on appropriate soil temperatures and moisture. In addition, characteristic of the soil, including the availability of nutrients, organic matter to retain moisture and an appropriate pH for plant growth are also important. Any or all of these factors may be limiting for plant growth on dunes.

Interactions of soil moisture, temperature, aspect and contours of the land have been shown to affect species and community distributions. Even though surface layers of

sand on dunes were dry, Pool (1916) noted moist sand was always found at a depth of 10 cm and questioned whether it was due to capillary forces drawing water from lower depths or to internal dew formation. He further observed that evaporation rapidly dried the soil surface, leaving loose sand as a dry mulch which protected lower depths from further evaporation. Surface soil temperatures in different communities were progressively cooler with increasing vegetation cover (Pool, 1916).

Salisbury (1952) discussed moisture in dune sands and attributed it to internal dew formation, the result of warm moist air coming in contact with cool sand grains which act as condensation surfaces. Willis et al. (1959) discounted Salisbury's interpretation since soil temperatures in the latter's data did not fall below the dew point. An alternate theory was suggested whereby moisture movements in sand were determined by thermal gradients independent of dew formation. Internal dew formation and upward movement of moisture in sand were further discussed by Ranwell (1972) , but no conclusions were drawn about their relative contributions to sub-surface soil moisture.

Salisbury (1934) studied the effects of vegetation, sand color and topography on dune temperatures. In general, on yellow dunes, increased vegetation slightly reduced soil surface temperatures. On soils with more developed vegetation and darker color, temperatures slightly exceeded



those on yellow dunes. He also found greater heat transference on darker soils owing to their higher content of organic matter and soil moisture levels. This greater heat transference gave warmer subsurface temperatures on darker soils than on light colored dune soils.

Willis et al., (1959) felt water supply and high temperatures were limiting to plant growth in the summer on Braunton Burrows. They observed large daily temperature fluctuations in the upper 60 cm of sand although the magnitude of fluctuations decreased with progressively greater depths. They also observed a reversal of the temperature gradients at night where surface and upper level temperatures fell below those at deeper levels.

Studies on North Carolina coastal dunes (van der Valk, 1974a) found soil temperatures at 10 cm depth were usually higher than air temperatures by  $1^{\circ}$  to  $5^{\circ}$  C. Weekly mean ranges were  $4^{\circ}$  to  $10^{\circ}$  for air and  $5^{\circ}$  to  $11^{\circ}$  for soil at 10 cm. Soil moisture measured at 20, 40, and 60 cm showed no significant differences and averaged 3.5%. It was concluded that soil temperatures and soil moisture had little impact on the functioning of the zonal ecosystem.

Soil moisture and temperature were observed on a prairie by Steiger (1930). Comparisons of clipped and natural areas revealed less moisture at 20 to 30 cm in clipped areas but 1 to 3% more moisture at lower depths. Soil temperatures at a depth of 8 cm were  $2^{\circ}$  C lower under plant cover than under clipped areas.

Differences in litter affected soil temperatures in a Missouri tall-grass prairie (Zimmerman and Kucera, 1977). Goldenrod communities had loosely packed litter while grass communities had tightly packed litter. Soils under goldenrod had higher temperatures which followed air temperatures more closely than under the grass communities.

A biomass study on a mixed grass prairie in North Dakota (Lauenroth and Whitman, 1977) showed a combination of air and soil temperature and vapor pressure deficit accounted for 99% of the variability in the above-ground biomass.

Ayyad and Dix (1964) have a review of micro-environmental effects on vegetation in their study of Saskatchewan prairies. Their findings indicated that soil temperature and soil moisture varied significantly with slope and aspect while air temperature and vapor pressure deficit did not. Vegetation was a significant factor in the lower air and soil temperatures found in the prairie compared to the bare sites.

Jamison (1956) studied factors governing soil moisture and found additional organic matter increased the water storage capacity of sandy soil, but at the same time decreased its wettability and was therefore of little value in improving soil moisture conditions. He also noted that soil moisture depended upon vegetation and climatic factors. Vegetation factors were drought resistance, rooting depth and ramification, plant vigor, and growth stage. Climatic factors included air temperature, humidity, fog, wind, and sunlight.

A comparison of dune and slack soils indicated much more organic matter in slacks and this was associated with moisture in the soil (Ranwell, 1959, 1972). Further comparisons revealed a higher moisture content on open dunes as opposed to fixed dunes, due to internal dew formation and a lack of vegetation with high transpiration rates to deplete the water (Ranwell, 1959).

In addition to soil moisture, soil fertility is a major factor affecting all plant communities, especially those of nutrient-poor ecosystems such as dunes. Olson (1958a) noted that soils with low fertility favored species with low nutrient requirements. These plants recycled few nutrients to dune litter and nutrients were, in turn, rapidly leached from the sand and not available to support more extensive vegetation. Work on Braunton Burrows confirmed that nutrients were lost by leaching and revealed that the observed low levels of nitrogen, phosphorus and potassium had important effects in determining vegetation patterns (Willis et al. 1959). Further work on soils of the same area, with turf transplants and tomatoes, found slightly greater natural levels of nutrients in stabilized dunes compared to blowouts. All soils had adequate supplies of minor nutrients and these nutrients were not limiting to plant growth. Willis (1963) added nutrients to dune communities in the field and concluded that the short growth and open habit of such communities was due, in part, to nutrient deficiencies. Chandapillai (1970) found dune stands characterized by low levels of nitrogen and

potassium which affect community composition. However, studies on a coastal foredune (van der Valk, 1974a) and a Wisconsin prairie (Curtis, 1955) indicated that nutrients had little influence on species distribution.

Nutrients in rainfall have been shown to be significant in the nutrient cycles of oligotrophic sites (Allen et al., 1968) and dust can account for 10 to 27% of the cations in rainfall (van der Valk, 1974b). In spite of relatively large cation inputs into dune systems the cation exchange of sand is low and nutrients leach through the upper 60 cm rapidly (Boyce, 1954).

Many studies have shown an increase in organic matter and a decrease in pH with increasing colonization and vegetation development (Pool, 1916; Salisbury, 1925; Ranwell, 1959, 1972). Organic matter is credited with giving soil an increased ability to retain moisture and nutrients. It also modifies and improves aeration characteristics and increases the base exchange capacity (Olson, 1958a). Deeper soil depths on dunes were found to have less organic matter and higher pH values than surface levels (Ranwell, 1959).

Many researchers have performed mechanical analyses of soils but few have drawn any conclusion from the data. Pool (1916), Olson (1958a), and Hanson and Whitman (1938) found particle sizes varied between sites while Ranwell (1959) found a homogeneous composition in dune soils. Hanson and Whitman's research showed soil heterogeneity corresponded to vegetational heterogeneity but the varying soil particle sizes were not assumed to be responsible for community types.

Succession and Vegetation Patterns. North American work on dunes and sand hills has been conducted on sea coasts, large inland lakes and glacial deltas which have been blown into dunes. The latter usually support grassland vegetation. However, much of this research is not related to succession but reflects the economic use of the land for range management purposes or forage production, and the tolerance to drought (Hanson, 1938; Albertson, 1941; Sarvis, 1941; Clarke et al., 1942; Albertson and Weaver, 1944). Many other studies have given descriptive treatments to plant communities (Moss, 1944; Hanson, 1955; and Rothenberger, 1976).

Successional studies have been conducted on the sand dunes of Lake Michigan by several workers. Cowles (1899) examined plant communities on embryonic dunes, upper beaches, and terraces and fossil beaches. Olson (1958a,b,c) continued Cowles' work with discussions of edaphic changes and the geomorphology of dune development. Van Denack (1961) studied the communities and soil characteristics of open stabilized dunes, forested ridges and sloughs on the western shore of Lake Michigan. Morrison and Yarranton (1973, 1974) also discussed long term successional development on the shores of Lake Huron.

Succession on coastal dunes has also been described by several workers. Kumler (1969) identified nine successional stages from scattered plants on shifting sand to near-climax dune forest on the sea coast of Oregon. McBride and Stone (1976) described successional stages based on the percent cover of the dominant species, and age structure of stands

where trees were present. In addition, they discussed changing edaphic factors. Lamoureux and Grandtner (1977) reported nine phytosociological groups arranged in zones parallel with the shoreline.

Successional processes on inland dunes and sand hills are less well known than those of the Great Lakes and sea coasts but have been described in Nebraska (Pool, 1916; Tolstead, 1942), in Colorado (Ramaley, 1939), in North Dakota (Burgess, 1965), and in Saskatchewan (Hulett et al., 1966).

In contrast to North American researchers, the British have been much more prolific in describing succession on coastal dunes. Among the writers have been Hepburn (1952), Ranwell (1959, 1960), Salisbury (1925, 1952) and Willis et al. (1959). Due to the widely differing climates, soil types and species between North America and Britain, however, it is frequently difficult to relate the British information to the ecosystems found in the middle of the North American continent. Only the broad principles of succession are applicable.

Successional stages are frequently analyzed by examining different zones or spatial arrangements of communities (Gleason, 1927) and interpreting the spatial arrangement in temporal terms. Vegetational patterns on dunes may appear in either zonal or heterogeneous forms and result from a complexity of factors which are not always readily discernible. Zonal patterns are found in areas with well defined environmental or topographical gradients or with species of narrow ecological amplitude and have been

described by Oosting and Billings (1942), Salisbury (1952), and Lamoureux and Grandtner (1977).

Successional stages at Braunton Burrows (Willis, 1959) did not follow the classical zonal pattern of colonization of a mobile sand surface, followed by the development of a grass turf, and final establishment of Calluna heath. Instead, the pattern revealed a complex mosaic determined by the high mobility and varying rates of dune movement.

Van Denack (1961) observed that sands in her study on the shores of Lake Michigan had a common origin but supported heterogeneous vegetation. The heterogeneous patterns were related to the sorting of species along gradients of wind, moisture, nutrients, shifting substrates, organic matter, light intensities and combinations of these.

As in all cases of primary succession, the initial establishment of plants on open dunes depends upon several factors including the proximity to parental seed sources, the ability to germinate quickly and establish deep root systems and the ability to withstand the effects of blowing sand. Hepburn (1952) discussed species found on young and older dunes and related the pioneer species to the proximity of the parental seed source and their ability to survive mobile sand. Chadwick and Dalke (1965) found Amelanchier alnifolia and Symphoricarpos vaccinoides on dunes protected from the wind and stated that their establishment was not dependent upon soil nutrients but rather was related to the degree of sand movement, seed introduction and germination, and seedling survival.

Blom (1976, 1977) reported that mechanical resistance of dune sands was an important factor in the emergence and establishment of seedlings. Their establishment was most successful on loose soils if sufficient moisture was available. Most authors working on dune succession have noted the ability of seedlings and mature plants to withstand burial and abrasion by blowing sand (Hulett et al., 1966; Salisbury, 1952).

The ability of species to become rooted well enough to obtain sufficient moisture and to avoid being undermined by the wind has been studied by numerous researchers. An early study by Waterman (1919) described root systems of dune species and observed varied reactions of different species to the same environmental conditions, although within a species root behavior was uniform. Wells and Shunk (1931) discussed habitat factors on the North Carolina coast and concluded that roots in xeric species have the ability to continually grow for water in the presence of poor nutrient status soils and low water levels, but mesic species find it impossible to become established. The effects of dry soils were compounded by dry air conditions caused by heat reflection from the white sand.

Kumler (1969) studied the coastal dunes of Oregon and found that pioneer plants reproduced vegetatively from rhizomes. There were distinct plant communities with successional stages. Hulett et al. (1966) described the plant communities in dune areas of Saskatchewan noting the dominance of rhizomatous species on unstable areas.



Tolstead (1942) studied dunes in Nebraska and found dominant species on the dunes were distributed in communities dependent on the aerial environment and the ability of rain to infiltrate the sand without loss from runoff and subsequent evaporation. He also described individual species in terms of rooting characteristics and growth habit.

The ecology of mixed grass prairie in Canada, its major communities, and characteristics of dominant species, including those found on sand hills, were described by Coupland (1950). Rooting characteristics of major grassland species in Saskatchewan were discussed by Coupland and Johnson (1965). On sandy soils xeric species had shallow root systems compared to mesic species which developed deep roots. Lateral root systems of grasses were the same in sandy and loam soils while forbs developed more extensive systems in sandy soils than in loams.

Brief discussions of sand hill and sand dune vegetation in the Northern Great Plains have been written by Coupland (1961) and the sand hills in northeastern Colorado were described by Ramaley (1939). Weaver and Fitzpatrick (1932, 1934) considered dominant species of the tall grass prairie in terms of their life histories, rooting and growth habits and interrelations with neighboring species. These studies describe many plant species found in the Carberry Sand Hills and are useful in relating the Manitoba ecosystem to similar systems found elsewhere.

Grasses are not always the dominant species found or studied on dunes. Many British dune systems have mosses and lichens as dominant species in early seral stages. Watson (1918) listed plant associations in dune areas of varying stability and noted that the most abundant plants of sand hills were often cryptogams. Bryophytes were observed to have xerophytic characters and changes in lichen communities were indicators of sand mobility. Richards (1929) observed that bryophytes and lichens at Blakeney Point did not colonize the sand until it was partially stabilized. He also described the species and their morphological adaptations on pioneer grey dunes.

The ability of some mosses to survive burial and reproduce by new shoots with rhizoids was described by Leach (1931). Further work on the ability of mosses to withstand burial by sand was conducted by Birse et al., (1957) and Oliver (1971). Growth forms of bryophytes and their relationship to environmental factors have been discussed by Birse and Gimingham (1955). Initial colonization is carried out by short turf growth forms followed by mat forms in fixed dunes and weft forms in dune pastures.

Alvin (1960) discussed lichen succession which occurred in a zonal pattern on dune ridges and was closely related to changes in soil pH and development of higher plant communities.

Few North American researchers have discussed lichens or bryophytes when describing dune or grassland communities.

Either their role is not as great in these communities or the workers have not had an interest in non-vascular species. A notable exception is a description of the Andropogon scoparius-Cladonia association observed in the sand plains vegetation of Connecticut (Olmstead, 1937). Dowding (1929) also described the cryptogamic vegetation found beneath the pines on sand hills in Alberta.

#### TRAMPLING IMPACTS

Approaches to impact studies vary and include studying existing damage, observing damage in new areas caused by normal recreational use, and designing experiments to quantify use and damage on new areas. Some of the earliest publications described field observations. Bates (1935, 1938) noted that the chief factors affecting vegetation in paths were the mechanical effects of treading caused by the pressure and twisting motion of the foot, and puddling of soils under wet conditions. Life forms of plants able to tolerate trampling were found to be annuals and geophytes. Davies (1938) discussed the vertical, horizontal, and semi-rotary twist forces of trampling. He also described plant species found in areas of heavy traffic and low soil fertility.

The majority of studies have centered around assessing existing damage in a variety of ecosystems. LaPage (1963, 1967) discussed the effects of camping and noted that small plants with linear leaves were more tolerant than larger species with succulent leaves. He also noted that the inten-

sity of use was not directly correlated with a reduction in vegetation density as some plants thrived when competition from trample-sensitive species was removed.

Degradation of trails in the Rocky Mountains was investigated by Dale and Weaver (1974). They found trail widths increased linearly with logarithmic increases in the number of users. Meadow trails were slightly wider than forest trails with the same amount of use. Further studies by Weaver and Dale (1978) examined the different effects of hikers, motorcycles and horses in meadows and forests of the mountains. Hikers were more damaging going downhill than uphill and shrubby vegetation was more rapidly damaged than grassy communities.

Scenic overlooks and car park areas in alpine tundra systems of the Rocky Mountains in Colorado were assessed for damage by Willard and Marr (1970). They devised a scale of impacts from 0, no impact; to 5, ecosystem destroyed with 0 to 5% of the natural vegetation cover remaining. Sites studied varied from areas opened in 1920 to areas opened during the study period. The ability of the alpine tundra to recover and regenerate was monitored with the aid of enclosures in trampled areas (Willard and Marr, 1971).

Dune systems and the effects of trampling have been studied by Liddle (1975). He theorized that vegetation became more tolerant to trampling with progressive stages of plant succession. Liddle and Greig-Smith (1975b) discussed dune vegetation and observed that the relative proportions of dicotyledons and monocotyledons changed with different

intensities of trampling. Monocotyledons decreased and dicotyledons increased under moderate trampling, but the reverse was found when the trampling intensity was increased.

Boorman (1977) used a combination of aerial photographs to map vegetation and path widths to determine which communities were most vulnerable to trampling on a dune at Winterton, Norfolk, England. Goldsmith et al. (1970) studied recreational impacts on the Isles of Scilly with a variety of techniques including vegetation maps, map-questionnaires for visitors, and recording visitor activity by photographs, electronic counters, and direct observation. This was combined with vegetation and soil data to make predictions about future impacts and management.

Trampling damage has lead to an examination of environmental factors as well as the vegetation aspects. Kellomaki and Saastomoinen (1975) found the relationship between soil fertility and trampling tolerance was curvilinear, such that the trampling tolerance of vegetation on soils of very low or very high fertility was less than vegetation on medium fertility soils. Numerous studies have related soil compaction, increased soil bulk density, and water retention to increased trampling intensities (Chappell et al., 1971; Liddle and Moore, 1974; Liddle and Grieg-Smith, 1975a; and Crawford and Liddle, 1977). Compaction and mechanical resistance of soils were found to affect the germination and establishment of Plantago seedlings on coastal dunes (Blom, 1976). A study of the microclimate of dune tracks (Liddle

and Moore, 1974) revealed that vegetation removal increased soil temperature ranges by  $15^{\circ}$  C but compaction in a dry area reduced them by  $7^{\circ}$  C.

Experimental approaches to trampling studies have involved mechanical devices to imitate the effects of trampling, and trampling new areas at predetermined intensities. Wagar (1964, 1967) used tamping devices and a ridged roller to simulate trampling. The tamp was also employed by Kollo-maki and Saastomoinen (1975) and the roller by Cieslinski and Wagar (1970). Establishment of trample plots which are trampled over a period of time at known intensities have been reported by researchers, among these are Liddle, 1973; Cordes et al., 1975; Boorman, 1977; Shay and Shay, 1979.

The need to anticipate the effects of recreational impacts has lead to the development of predictive models for trampling impacts. Wagar (1961) developed a slide rule to estimate vegetation survival. The slide rule was based on the percentage of low growing vegetation consisting of grasses and woody vines, the percentage of sunlight, and the dry weight of undisturbed low growing vegetation. Cieslinski and Wagar (1970) found variables which could be determined from aerial photographs were as useful in predicting vegetation vulnerability as those collected on the ground. Significant and consistent variables in the predictions included slope percent, aspect, elevation and an interaction factor between slope percent and aspect. Cole (1978) devised a measure of floristic dissimilarity of species composition between trails

and adjacent areas. Larger dissimilarity values indicated more significant impacts from trampling.

## CHAPTER 2

### COLONIZATION AND SUCCESSION IN THE CARBERRY SAND HILLS



## DESCRIPTION OF THE AREA

The Carberry Sand Hills or Bald Head Hills lie at  $49^{\circ}40'N$ ,  $99^{\circ}20'W$ ; 136 km west of Winnipeg and 56 km east of Brandon, Manitoba. During the period of deglaciation, 14,000 years ago, the Assiniboine River deposited gravel, sand and silt over a large area as it flowed into Glacial Lake Agassiz. The resulting delta was 135 km long, 70 km wide and 80 meters deep (Davies et al., 1962). Sand from the delta was formed by the wind into dunes, the majority of which are now covered with vegetation, although about  $30 \text{ km}^2$  are predominantly bare. New dunes have a parabolic form with a long, gently sloping, windward side and a steep leeward face up to 17 meters above succeeding dunes. Older dunes have slowly eroded leaving gently rounded forms.

The Sand Hills lie in a region of humid continental climate characterized by long cold winters and short cool summers (Thorntwaite, 1931). Temperatures reach a high in July, (mean  $19.7^{\circ}C$ ), and a low in January, (mean  $-18.6^{\circ}C$ ). Most precipitation falls as rain (36.0 cm), with the remainder as snow, (14.2 cm in rain equivalent).

The rolling, mixed-grass prairie is dotted with Picea glauca and groves of Populus tremuloides. According to Rowe (1972), the sand hills lie between the mixed-wood and aspen-oak sections of the boreal forest. Bird (1961) described the area as aspen parkland and Ritchie (1976) considered the sand hills as part of the transitional zone between parkland and boreal

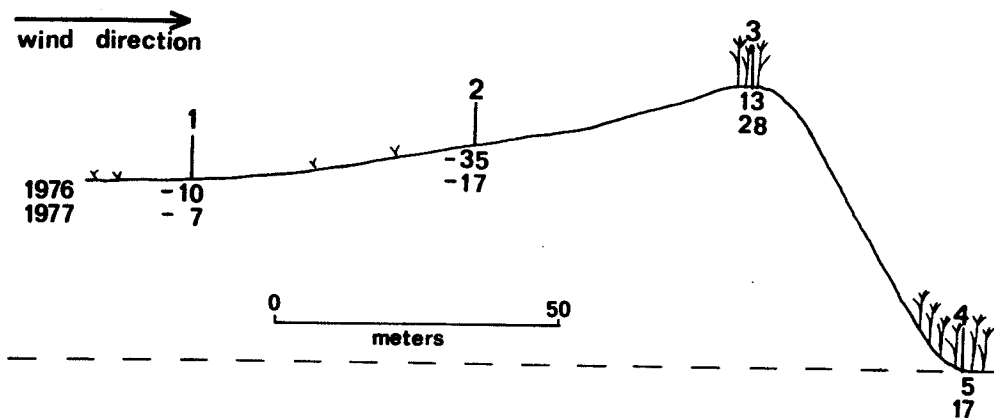
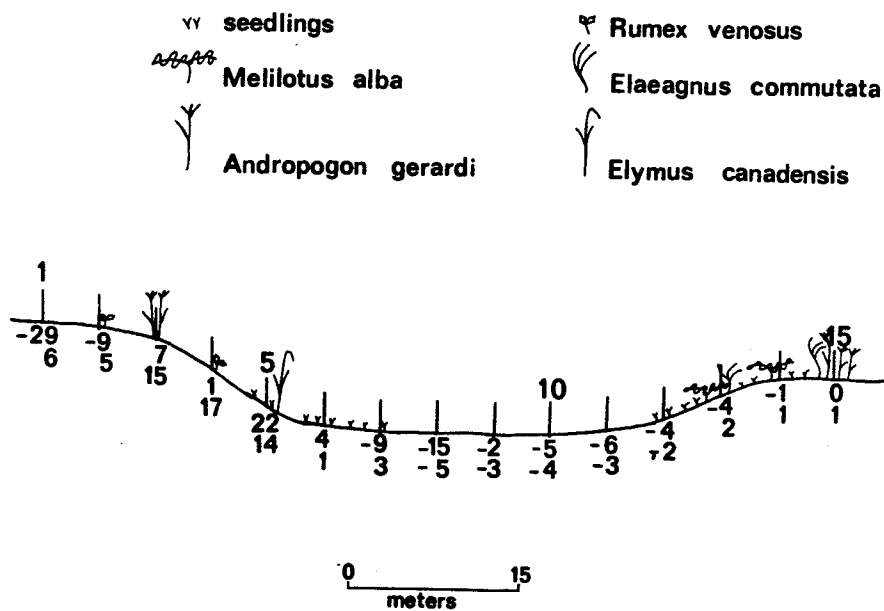
forest. Ritchie described the historic development of sand hill vegetation beginning with a Picea forest with Juniperus and Artemisia 10,000 to 14,000 years B.P. This was followed by a treeless prairie period. Picea reoccupied the area with Juniperus and Arctostaphylos uva-ursi about 1500 to 2000 B.P. The reappearance of Picea was interpreted as a recovery from low populations prior to 4000 B.P. or more likely as a southward extension of Picea from Riding Mountain National Park, 130 km north of the sand hills.

## METHODS AND MATERIALS

From aerial photographs and ground reconnaissance, four study areas were selected. These ranged from bare and little colonized dunes, (Site I,) through two intermediate communities on stabilized dunes, (Sites II and III), to prairie, (Site IV). At the beginning of the growing season (mid May, week 0) temperatures, rainfall and soil moisture in each site, and sand movement on Site I were recorded bi-weekly. Plant communities were surveyed every fourth week, (five times during the growing season). Soil samples were collected from each site in the spring and fall.

Dune Movement and Colonization. Long term dune movement on Site I was assessed by examining 1948 and 1974 aerial photographs. A dot grid overlay on these photographs was used to determine the amount of plant cover and to calculate the rate of colonization. To measure current rates of movement, four stakes, two meters long, were placed a meter deep and 50 meters apart on one dune parallel with the prevailing wind. Fifteen stakes, three meters apart, were placed perpendicular to the prevailing wind across a dune trough (Fig. 1). Measurements from stake tops to the sand surface indicated the extent of erosion or accumulation.

Figure 1. Summer erosion and deposition of sand on open dunes, (Site I). In a. stakes 1-4 are parallel to the prevailing wind, and in b. stakes 1-15 are perpendicular to the prevailing wind. Values (cm) for accumulation and erosion are indicated below the numbered stakes.

**a****b**

Environmental Factors. From early May, at each site, air and soil temperatures were recorded at hourly intervals by Grant recorders with probes located 50 cm above the ground, on the soil surface, and at 5, 10, 20 and 30 cm depths. Bi-weekly the moisture status of the soil was estimated as the percent available soil moisture using a BN-2B Bouyoucous moisture meter, and CEL-WFD gypsum blocks installed each spring at 5, 10, 20 and 30 cm depths. Accumulated rainfall was measured bi-weekly in a wedge-type gauge placed 1.5 meters above the ground, and containing mineral oil to prevent evaporation.

Four soil pits were dug at each site to provide data on soil characteristics, profiles and rooting depths. As the pits exhibited poorly developed profiles, soil samples were collected for analysis from the upper 5 cm and between 45 and 55 cm, the lower level of the major rooting zone. Organic matter content was determined by loss on ignition. Conductivity and pH were measured using a Radiometer conductivity meter CDM-2e and Radiometer pH meter No. 29 respectively, from a soil paste of 75 ml water and 100 g soil. Nitrate nitrogen and available phosphate and potassium were determined by the Manitoba Provincial Soil Testing Laboratory. Soil texture was determined by sieving and by the rate of settling from suspension (Kilmer and Alexander, 1949). An analysis of variance and Duncan's multiple range test were calculated for edaphic characters to ascertain variation within and between sites and soil depths.

Vegetation. Vegetation at each site was sampled bi-weekly with 25 randomly placed 25 x 25 cm quadrats. Species cover, sociability and percent bare ground and litter were recorded using a modified Braun-Blanquet (1932) scale. Class mid-points were used to calculate percent cover. Due to difficulties in identification, lichens and immature sedges were ascribed to their appropriate genera, while mosses (except Tortula ruralis) were considered collectively. Nomenclature follows Scoggan (1957) for vascular plants, Crum (1976) for mosses and Hale (1969) for lichens.

A prominence value,  $(\text{cover} \sqrt{\text{frequency}})$  (Beals, 1960), was calculated for each species and bare ground for each sampling period. The maximum prominence value (PV) attainable is 1000. All PV's greater than 5 were graphed to compare behavior within and between sites and years. Sites were ordinated (Bray and Curtis 1957) using species cover and percent bare ground. Calculations involved the four sites for the 5 sampling times each year. The end stands for the x and y axes were those with the greatest total dissimilarity values and with three similarity indices greater than 50% (Swan and Dix, 1966; Newsome and Dix, 1968). Placement of all other stands on the axes followed Beals (1960). A statistical test of the ability of the two axes to account for the variation was estimated by correlating the ordination interval with the dissimilarity values for randomly chosen community pairs (Mueller-Dombois, 1974).

## RESULTS AND DISCUSSION

Dune Colonization. A comparison of aerial photographs from 1948 and 1974, (Figs. 2 and 3), reveals that dunes in both the northern and southern series have been essentially stable for the past 26 years. In 1948, the dunes were bare except for sparse vegetation cover on some ridges and in hollows at the toes of leeward edges. A portion of the southern series (enclosed by the broken line on Fig. 2) had 27% of the surface colonized. By 1974 this portion was 68% vegetated. If a logarithmic rate of plant coverage in colonization is assumed, the dunes should be completely colonized by 1987. Assuming a linear rate of colonization the year would be 1994.

The pattern of vegetative colonization occurs on two scales. The larger scale is found on both dune series while the smaller scale occurs on individual dunes. Colonization and subsequent development of plant cover follow the prevailing wind from the northwest toward the southeast. Thus the total dune series is more vegetated in its northwestern portions and has less cover on leading edges. The pattern of vegetation on an individual dune is similar, as plant growth develops on lower portions of windward faces and progresses to the crest.

Periodic fires have affected colonization and subsequent community development in the peripheral stabilised area. In 1948 there were dense stands of white spruce surrounding the dunes, but most were subsequently destroyed by fires. Few spruce seedlings or young trees are now found due to a lack of open ground for germination and their inability to compete with other plants for water. Scoggan (1957) noted widely varying



Figure 2. 1948 aerial photograph of a portion of the Carberry Sand Hills. N and S refer to the northern and southern dune series. The three southernmost dunes used to calculate the rate of colonization are enclosed by the broken line.

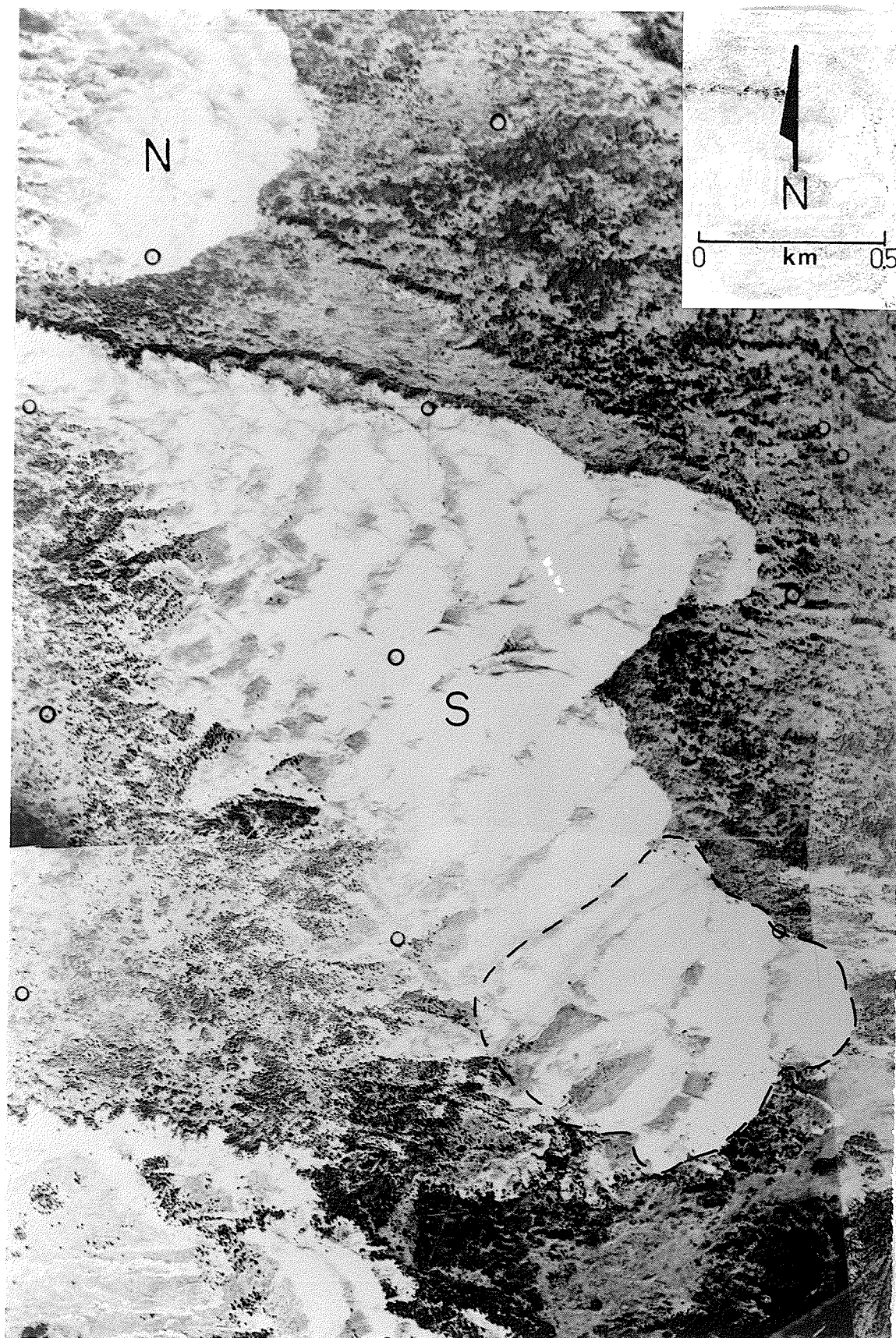
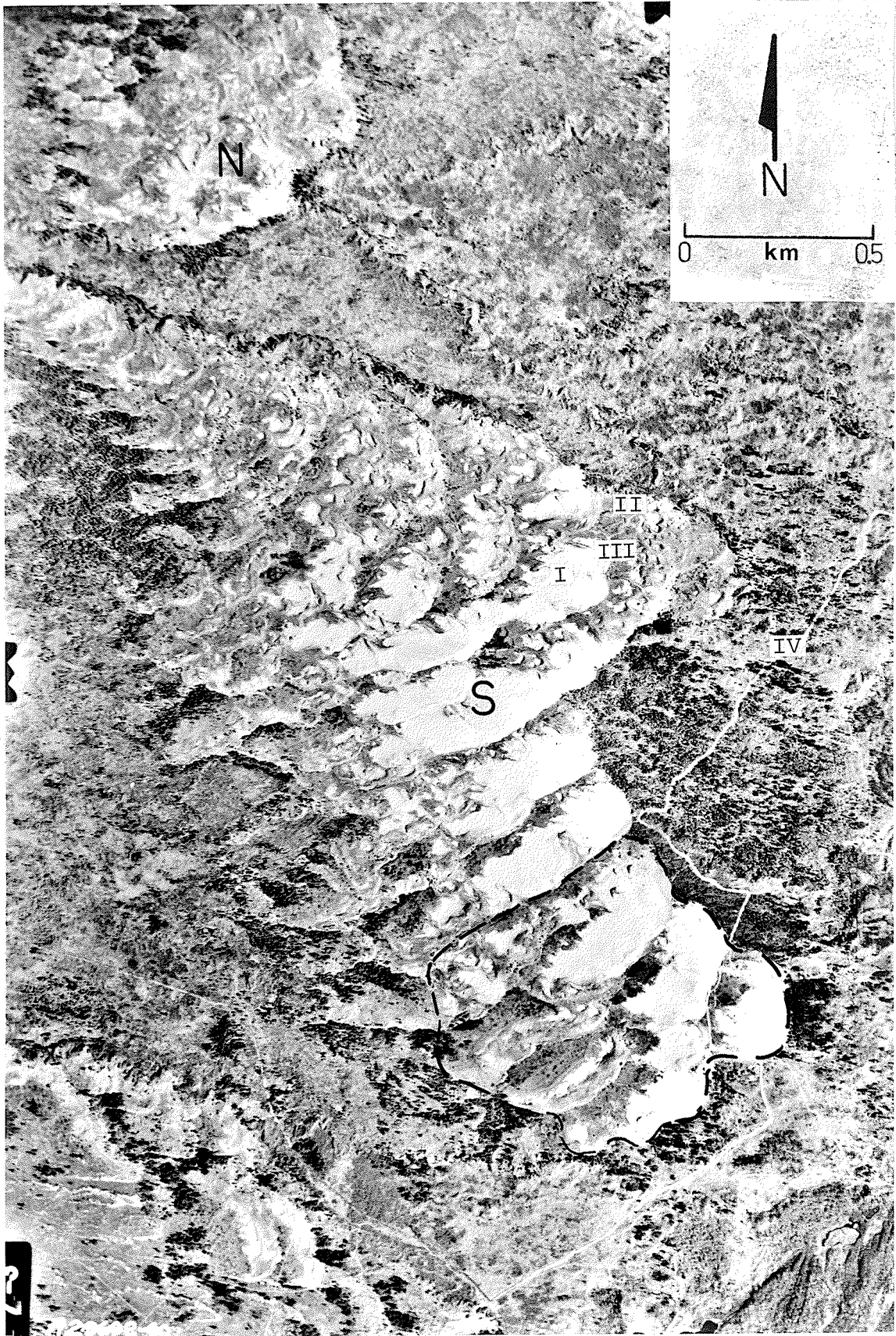


Figure 3. 1974 aerial photograph of a portion of the Carberry Sand Hills. N and S refer to the northern and southern dune series. The three southernmost dunes used to calculate the rate of colonization are enclosed by the broken line. Sites are marked I, II, III, IV, V.





seasonal precipitation, thick prairie sod and severe winters as factors affecting tree seedling survival in the area.

From initial ground reconnaissance it was observed that colonization of bare dunes, their final stabilization, and development of prairie were affected by wind, slope and aspect. Figure 4 illustrates the typical community structures found in the four study sites.

Active dunes, (Site I), have only 1 to 2% plant cover because low moisture in soil surface layers, high winds and blowing sand combine to abrade, undermine or bury seedlings of colonizing species. Long, gentle, windward dune slopes have few if any plants, except where they find some protection in the lee shadow of the preceding dune. Here, Lygodesmia juncea, Helianthus petiolaris and some grass seedlings may survive to reproduce vegetatively or by seed. On dune crests or ridges there are clumps of large bunch forming grasses, Andropogon gerardi and Oryzopsis hymenoides. Both species act in a limited way to trap and bind sand. Older clumps may be perched a meter above the surrounding dune surface, demonstrating their ability to withstand considerable erosion around their dense bases and root systems. On steep leeward sides of dunes, Andropogon gerardi, Rhus radicans and Cornus stolonifera extend up the slope by producing tillers and rhizomes when buried by moving sand.

Recently stabilized areas, (Site II), are 30 to 40% vegetated. Dominant species in order of decreasing cover are Koeleria cristata, Andropogon gerardi, Petalostemum candidum and Artemisia campestris. All grow in tufts or clumps, leaving

Figure 4. Communities found in a portion of Carberry Sand Hills:

- a) Site 1, sparse vegetation on open dunes, predominantly Lygodesmia juncea.
- b) Site II scattered, open community with Koeleria cristata, Andropogon gerardi, Petalostemum candidum and Artemisia campestris subsp. caudata.
- c) Site III community with Juniperus horizontalis (dark patches) Koeleria cristata and Andropogon gerardi.
- d) Site IV prairie with Picea glauca and Populus tremuloides.





up to 30 cm of bare sand between adjacent plants. Elaeagnus commutata is widely scattered with a frequency of 10% and cover of 1%, while Solidago nemoralis has twice the frequency and cover and is found in the interstices between the grasses with scattered plants of Lygodesmia juncea and Chrysopsis villosa. Breaks in the cover or disturbances to this community permit wind erosion.

Site III communities, the smallest in area, are found only in low lying, sheltered areas at the bases of leeward slopes. These sites have the greatest protection from the wind and growth resumes one to two weeks earlier in the spring due to the warmth radiated by bare leeward faces. This plant community with 50% cover, is more luxuriant and diverse than the preceding ones. Dominant species in order of decreasing cover are Koeleria cristata, Andropogon scoparius, Juniperus horizontalis, Andropogon gerardi and Solidago nemoralis. Less important species include Calamovilfa longifolia, Artemisia campestris, and Festuca ovina. Some species found only on this site include Oxytropis lambertii, Mamillaria vivipara, and Tortula ruralis. Tortula occurs in widely spaced colonies occupying areas up to several square meters. Under dry conditions it appears as a short, scurfy, brown mat but within seconds after the beginning of rain, the leaves unfold from around the stem and it becomes bright green. Mamillaria vivipara has a frequency of about 1%, and is relatively inconspicuous as its hemispherical stems are half buried in the sand and the grey-green color blends with surface litter.



The prairie community, (Site IV), dominated by a mixture of short grasses and sedges, has the greatest number of species and a cover of 70 to 80%. Unlike the previous sites, the remaining 20 to 30% is covered by litter with very little exposed soil. Here the effects of aspect and micro-climate are more evident. Southern or exposed slopes are covered by grasses and forbs while northern slopes support Populus tremuloides and associated shrubs such as Symphoricarpos albus. Dominant species of the grassland community include Juniperus horizontalis, found in widely scattered but large patches, and Stipa spartea, Carex spp. and Cladonia spp. which are more evenly distributed. Lesser species include Bouteloua gracilis, Andropogon scoparius, Selaginella rupestris, Artemisia frigida, and Lithospermum canescens. A wide variety of other species are also found but most have frequencies and cover values between 1 and 2%.

#### Environmental Factors

Sand and Dune Movement. Erosion and deposition of sand on the dunes is summarized in Fig. 1 (p.36). In 1976, sand stakes parallel with the wind (Fig. 1a) showed losses from the heel and midway to the crest, (stakes 1 and 2) and gains at the crest and leading edge (stakes 3 and 4). During the first winter, stakes 1 and 2 were blown down, but the crest and toe gained 111 and 48 cm of sand respectively. In 1977, stakes were repositioned as it had been observed that previous stakes were somewhat oblique to the prevailing wind. Again, there was a loss from heel and mid-crest stakes with gains on the

crest and toe. Discrepancies between amounts lost and gained over a season are a reflection of unequal surface areas and plant cover affecting erosion and deposition.

Movement of sand on stakes perpendicular to the wind direction (Fig. 1b) showed a net loss of sand on the trough sides, stakes 1 and 2, and in the valley, stakes 7 through 13. Furthermore, slopes on the left side in the diagram accumulated up to ten times more than the other side which was more extensively covered. Winds oblique to the trough, from the left in the diagram, were observed to carry sand from the upper edge down the side. This dry, loose sand provided an unstable slip-face compared with the opposite side which lacked a supply of sand for deposition and was better colonized.

Leeward edges of dunes were observed to move 15 to 20 cm a year. At a rate of 20 cm per year the Carberry dunes would have moved less than 5.5 meters in the 26 years elapsed between the aerial photographs studied. This is far less than other reported rates of movement for either inland or coastal dunes. Dunes on Lake Michigan move one to four meters a year (Cowles, 1899; Gates, 1950); in Idaho, three meters a year (Chadwick and Dalke, 1965); and coastal dunes, up to 24 meters a year (Ranwell, 1958). The slow advance of the Carberry dunes can be attributed to a lack of sand necessary for further accretion and movement, since the dunes and prairie to the northwest of the open dunes are stabilized and covered with vegetation.

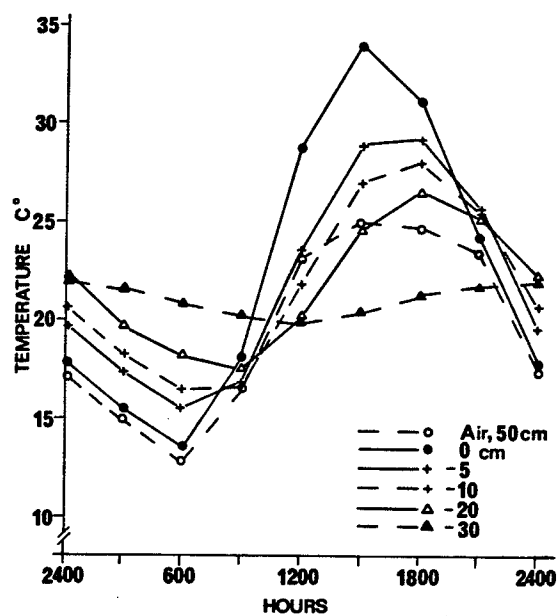
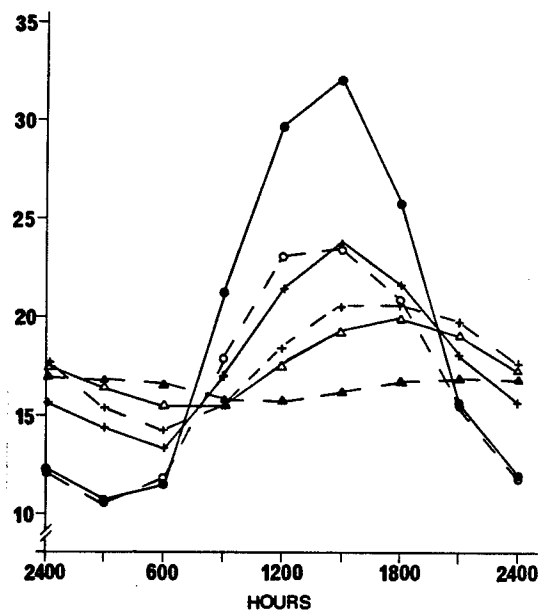
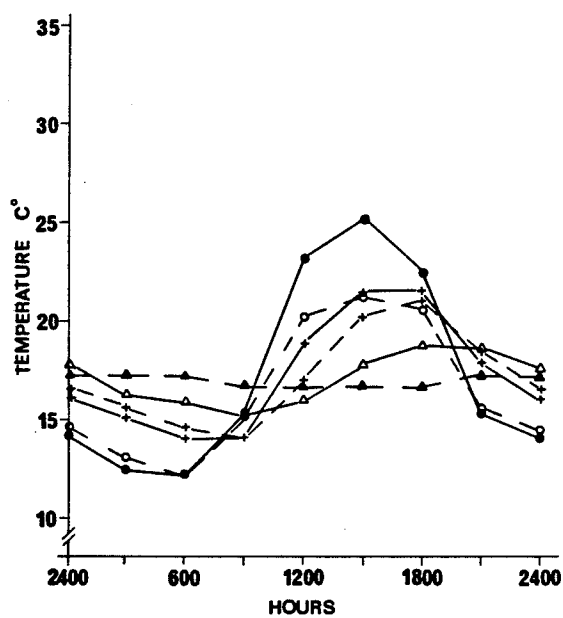
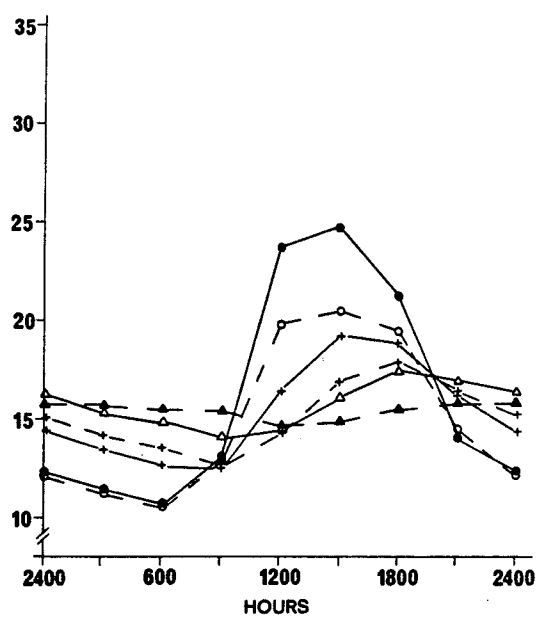
Air and Soil Temperatures. Throughout the growing season soil surfaces in all sites exhibited a large daily

temperature variation due to the low specific heat of the sand. Surface temperatures rose rapidly in the morning to a maximum in mid-afternoon and then fell abruptly (Fig. 5a, b). Soil surfaces in early summer had mean diurnal ranges of  $20^{\circ}\text{C}$  and  $22^{\circ}\text{C}$  on the dune and prairie respectively. Air temperatures 50 cm above the soil reached a mean maximum of  $34^{\circ}\text{C}$  on the dunes and  $32^{\circ}\text{C}$  on the prairie. Cooler sand and warmer air on the dunes compared with the prairie are a result of the light colored sand reflecting heat from its surface back into the surrounding air.

Dune soils at 5, 10 and 20 cm depths showed progressively less variation and reached their mean maxima about three hours after the air and soil surface. They also exceeded maximum air temperatures. At 30 cm there was a  $2^{\circ}\text{C}$  daily fluctuation with the maximum lagging 6 hours behind the soil surface. Due to the mulching effect of litter, prairie soils at 5 cm reached temperatures only slightly higher than the air; they were  $5^{\circ}\text{C}$  cooler than corresponding dune soils. At greater depths there was less variation and maximum temperatures were  $5^{\circ}$  to  $7^{\circ}$  lower than on the dune.

As the season progressed, the angle of radiation became more oblique to the surface, and daily temperature fluctuations decreased on both the dune and prairie, (Fig. 5c, d). Maximum temperatures declined from early summer by  $3^{\circ}$  to  $4^{\circ}\text{C}$  for air,  $7^{\circ}$  and  $9^{\circ}\text{C}$  for the surface, and  $6^{\circ}$  and  $7^{\circ}\text{C}$  at 5 cm for the prairie and dune respectively. In early summer, maximum temperatures from the surface down to the 20 cm depth on the

Figure 5. Averages of daily temperature variation over a two week period for Sites I and IV; where a. is Site I and b. is Site IV for the two weeks commencing June 24, 1976; and c. is Site I and d. Site IV commencing Sept. 2, 1976.

**a****b****c****d**

dune exceeded those of the air, but by fall only the surface maximum exceeded the air. On the prairie, only the maximum soil surface temperature significantly exceeded the air throughout the summer. By early fall, differences between maximum temperatures at comparable depths in Sites I and IV had narrowed to 2°C. Sites II and III produced intermediate temperature curves.

With differences of only 2°C to 3°C between mean minima and maxima on Sites I and IV, temperature may not be a major influence in accounting for community structure.

Although average maximum temperatures were within limits of normal plant metabolic processes, extremes of 45°C and 54°C for air and soil surfaces respectively were frequently encountered at Site I in July and August. Such extremes were not observed at the other sites.

Precipitation and Soil Moisture. The 30 year average rainfall at Shilo, 28 km northwest of the study area, is 26.7 cm for June through September. In 1976 rainfall at the study area was 21.4 cm, slightly below normal, while in 1977 it was higher than normal, 33.7 cm. Distribution of precipitation was not uniform but varied slightly between sites each time it rained. In 1976, Sites I, II and III received 20.7 cm precipitation while the prairie (Site IV) had 22 cm. In 1977, Site II had 30.2 cm and Site III 36.2 cm for the season. Usually, biweekly variations between sites were small, about 2 to 5 mm, but occasionally the difference was as much as 2 cm.

Soil moisture was measured as the percentage of field

capacity. At field capacity soils on Sites I, II and III, owe 18 to 19% of their weight to water while those on Site IV have 30% moisture. Thus, in the prairie, soils at field capacity have more water potentially available to support vegetation and this must be borne in mind when examining the soil moisture data.

Below-normal precipitation in 1976 led to depletion in soil moisture (Fig. 6) while increased rain in 1977 ensured that soils were at field capacity throughout the growing season. Site I had no moisture depletion in surface levels until week 15 and remained at field capacity at 20 and 30 cm depths until the end of the growing season. This was probably the result of the surface 5 cm of sand acting as a mulch coupled with an absence of plants to withdraw moisture.

In Site II moisture depletion began by week 9 in surface and lower layers and proceeded to the middle levels. In Site III most of the moisture depletion was at the top. Koeleria cristata, a dominant species on Sites II and III, is shallowly rooted (Coupland and Johnson, 1965) and may have utilized the water in the upper levels. The loss at 30 cm on Site II but not III may be associated with the long taproot of Petalostemum candidum which is well branched at the lower end (Weaver and Fitzpatrick, 1934). P. candidum was not found on Site III.

By week 11, prairie soils, (Site IV), were still at 100% capacity. However, by week 13, only the lower depth retained any moisture and within two more weeks that was also depleted.

It therefore appears that in sub-optimal conditions, the amount of plant cover strongly influences soil moisture patterns. The greater the development of plant cover the more evapotranspiration that occurs and the more rapid and deep the moisture loss. Overall, soil moisture influences species composition and growth. In 1976, dry conditions led to a mid-summer quiescent period for many plants. Above average rainfall, in 1977, however, ensured soils were always at field capacity and the plants did not enter a quiescent state until fall.

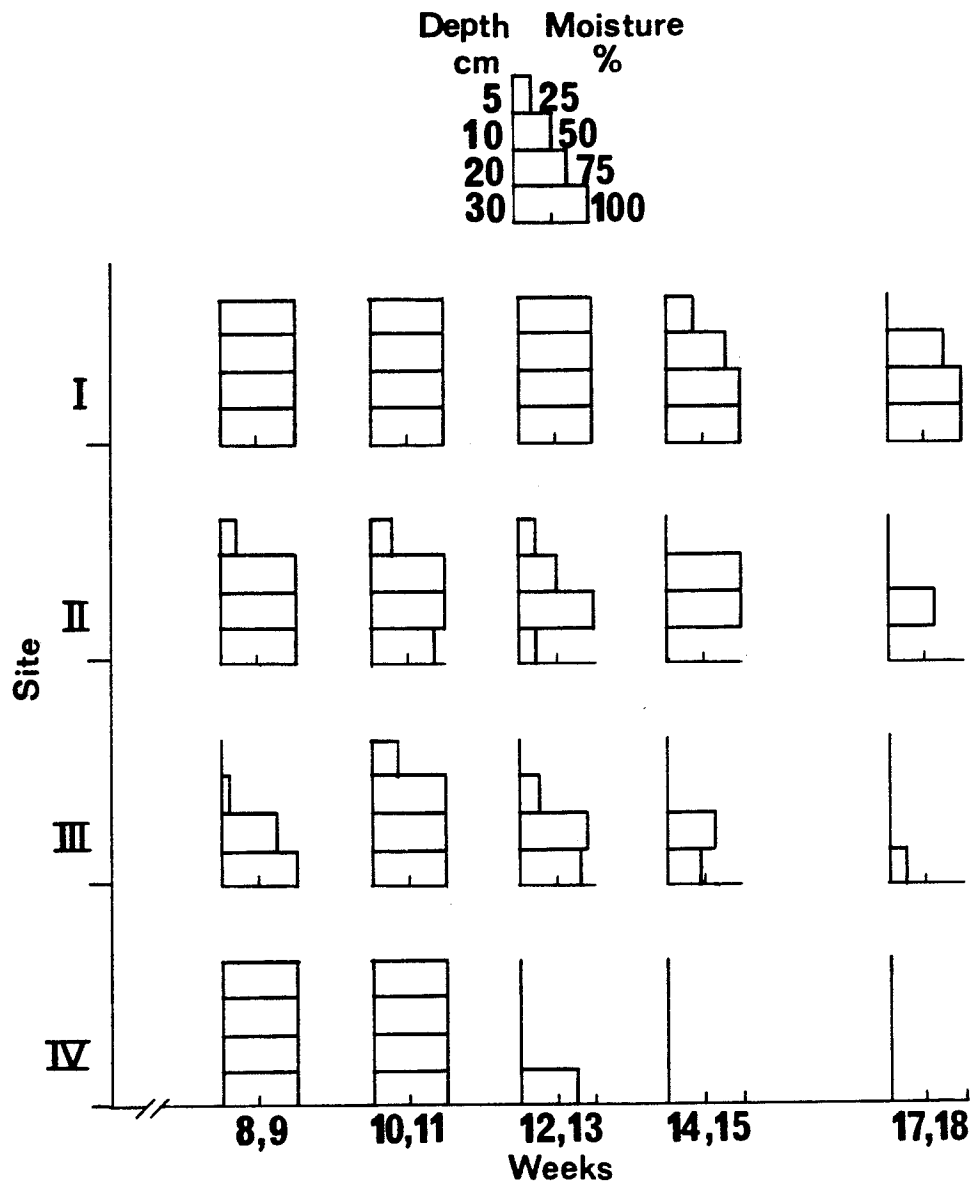
Soil Characteristics. Soil properties are summarized in Table 1. The high standard deviations are a result of small sample sizes (four determinations per site). They show overlapping values between adjacent sites indicating that the sites vary along a continuum. An analysis of variance and Duncan's multiple range test found few instances of statistically significant differences within or between sites.

A progression from the bare dunes to the prairie community revealed a decrease in pH from 8.3 to 7.6 in the surface layers with less of a decline in the lower levels. Except for Site I pH values increased with increasing depth.

Organic matter content in the surface layer increased from virtually none in the bare dune to 3.5% in the prairie. In all sites, apart from Site I, organic matter decreased with increasing depth. Increased organic matter produced progressively darker soil colors. Munsell (1954) soil colors for dry soils ranged from 2.5Y 5/4, (light olive brown) on Sites I and



Figure 6. Soil moisture in 1976 as the percentage of field capacity in Sites I through IV measured at the end of the two week periods indicated.



II; to 10YR 4/4, (dark yellowish brown), Site III; and 10YR 4/2, (dark grayish brown), Site IV.

Conductivity of all soils was low, probably due to strong leaching of salts and the low cation exchange capacity typical of sandy soils. A marked increase in conductivity in the surface layers was observed from Site I and IV but there was only a slight increase at the 40 to 60 cm depth.

Nutrient levels probably limit plant growth as they fall within or below the levels of 0.2% nitrate nitrogen, 5-12 ppm phosphorus and 75-100 ppm potassium which are regarded as low for Manitoba soils (Ehrlich, Poyser, and Pratt, 1957). Nitrogen increased at the surface and at 40-60 cm with increasing plant cover. Phosphorus was at a higher level on the surface of Site III than in other sites but remained at about the same value in deeper samples. Potassium increased in surface samples with increased vegetation but was relatively constant at 50 cm.

Soil texture was finer in the surface layer proceeding from Site I to IV. At the 40 to 60 cm depth all sites had similar textures. Denser vegetation is more effective in reducing wind speed and in trapping windborne dust and fine particles. Silt and clay each accounted for about 2% of the total soil weight on the prairie surface but these fractions were not found in the other sites. Although a very small portion of the total soil, the silt and clay may aid in retaining nutrients in the prairie soils.

The effects of environmental factors such as constant winds, low soil moisture, and low nutrient status of the soils

Table 1. Mean values and standard deviations for soil properties.<sup>2</sup>

Property	Depth cm	Site I bare dune	Site II intermediate	Site III	Site IV prairie
pH	0-5	8.3 ± 0.1	7.9 ± 0.2	7.7 ± 0.2	7.6 ± 0.2
	40-60	8.3 ± 0.1	8.3 ± 0.1	8.2 ± 0.2	8.0 ± 0.3
Organic matter (percent)	0-5	0.2 ± 0.2	0.6 ± 0.4	1.2 ± 0.4	3.5 ± 1.4*
	4-60	0.2 ± 0.1	0.3 ± 0.1	0.4 ± 0.3	0.7 ± 0.3
Conductivity (micro mhos)	0-5	106 ± 10	164 ± 38	241 ± 86	548 ± 238
	40-60	118 ± 9	113 ± 9	134 ± 30	171 ± 12
Nitrogen (nitrate) (ppm)	0-5	0.3 ± 0.2	1.1 ± 1.1	1.5 ± 0.6	4.9 ± 2.4*
	40-60	0.3 ± 0.1	0.4 ± 0	0.7 ± 0.6	0.9 ± 0.9
Phosphorus (available) (ppm)	0-5	1.2 ± 0.1	1.8 ± 0.7	3.7 ± 1.9*	1.4 ± 0.8
	40-60	1.6 ± 0.8	0.9 ± 0.1	1.3 ± 0.6	0.9 ± 0.2
Potassium (available) (ppm)	0-5	28 ± 5	30 ± 4	57 ± 21	95 ± 18
	40-60	27 ± 2	20 ± 2	26 ± 6	29 ± 9

Table 1. continued

Soil separate (1)	Particle sizes (% weight)					
Coarse sand	0.5 mm	0-5	9 ± 7	3 ± 2	4 ± 2	2 ± 1
		40-60	5 ± 4	7 ± 3	4 ± 2	2 ± 8
Medium sand	0.25 mm	0-5	70 ± 7	61 ± 6	48 ± 10	26 ± 2
		40-60	64 ± 5	65 ± 3	65 ± 17	59 ± 11
Fine sand	0.105 mm	0-5	20 ± 6	40 ± 4	40 ± 7	53 ± 6
		40-60	30 ± 8	27 ± 4	30 ± 16	37 ± 10
Very fine sand	0.053 mm	0-5	1 ± 1	1 ± 1	7 ± 4	14 ± 3
		40-60	1 ± 1	1 ± 0	2 ± 3	1 ± 1
Silt & clay	0.053 mm	0-5	0 ± 0	0 ± 0	1 ± 1	5 ± 2
		40-60	0 ± 0	0 ± 0	0 ± 0	0 ± 0

n=4

(1) United States Dept. Agriculture System (Buckman & Brady 1960).

(2) Ranges are in Appendix 1.

\* Significant at the 5% level from the other sites.

combine to adversely affect the vegetative colonization of the dunes. Wind is a continual factor on the open dunes where in a strong wind seedlings may be rapidly undermined or buried by blowing sand. In areas of sand deposition, both Andropogon gerardi and Oryzopsis hymenoides were able to tolerate 5 cm of burial with no apparent ill effects and to expand by tillers and rhizomes. The ability of certain grasses to withstand burial and erosion has been observed repeatedly on dune systems around the world. Perhaps the best known is Ammophila arenaria where regenerative capabilities depend upon a constant addition of sand (Ranwell, 1958; Willis et al., 1959). Whereas Carberry Sand Hill grasses are able to tolerate some burial, it is probably not a necessity for their continued survival.

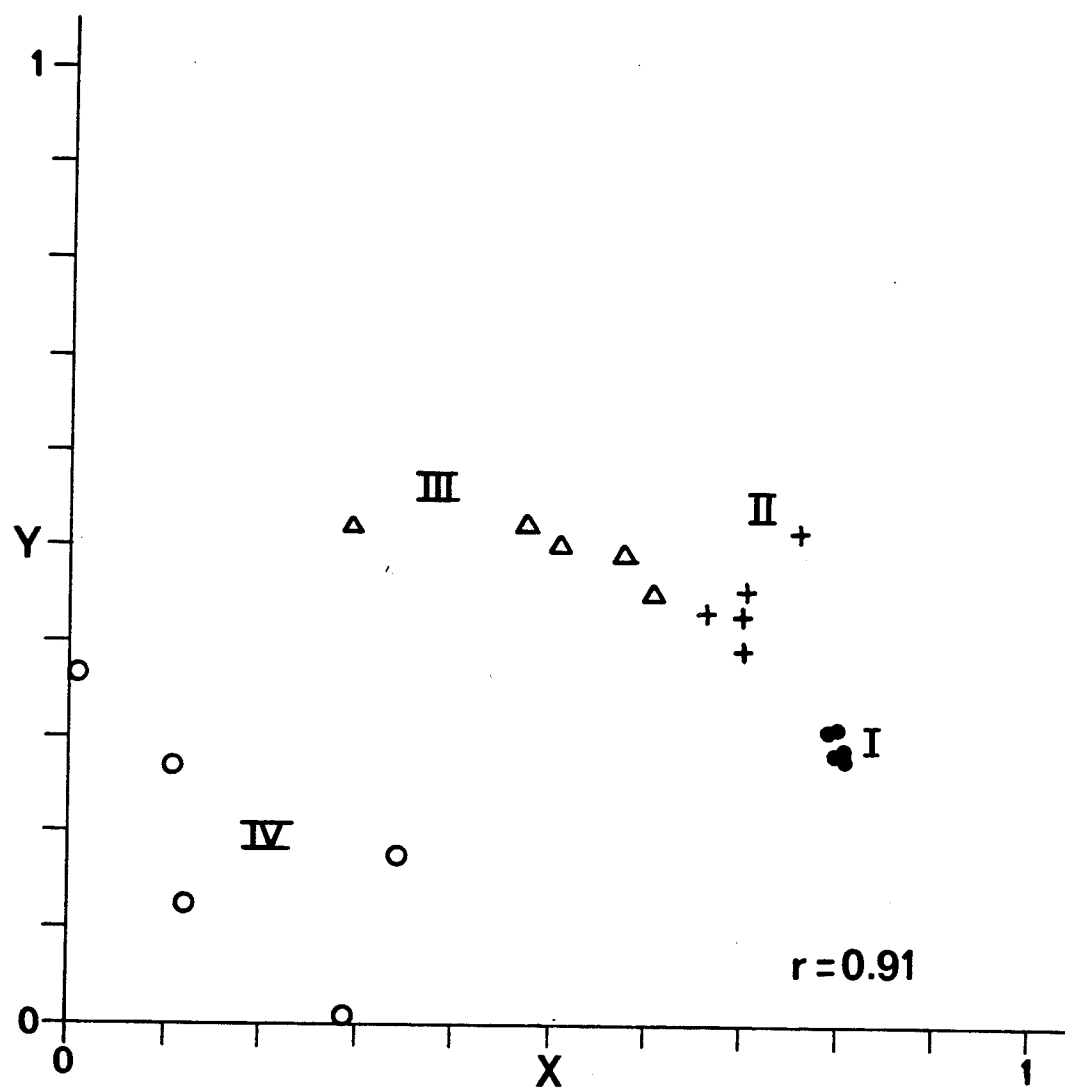
In spite of high evapotranspiration on the dunes and prairie, caused by wind and heat, no wilted plants were noted. However, the open structure of new and intermediate dune communities and the effects that various rooting depths have on soil moisture depletion indicate that moisture can be a limiting factor in these communities. This was demonstrated by the induced early dormancy caused in the first year by the dry conditions. Willis et al. (1959) also found soil moisture was a limiting factor in plant growth on dunes, although van der Valk (1974a) noted that soil moisture was not a factor in determining zonal vegetation on coastal dunes. The results found here also concur with those of Ayyad & Dix (1964) who noted that species distribution on Saskatchewan prairies was affected by soil moisture and heat regimes.

Increases in organic matter and decreases in pH with increased dune colonization and community development, such as observed here, have been reported by numerous other workers (Salisbury, 1925; Ranwell, 1959; and McBride and Stone, 1976). Organic matter has frequently been credited with increasing the ability of soils to absorb and retain moisture (Olson, 1958a). Low nutrient levels in dune soils such as those in the Carberry Sand Hills, are related to the low cation exchange capacity of sand and strong leaching. Olson (1958) also attributed low soil fertility to vegetation with low nutrient requirements that contributes only small quantities of nutrients to dune litter. Coastal sand dunes at Braunton Burrows were shown by Willis and Yemm (1961) to be deficient in nitrogen and phosphorus. Dunes at Newborough Warren have low levels of nitrogen and potassium (Chandapillai, 1970).

Community Ordination. An ordination of 1976 community data (Fig. 7) revealed that community structures and successional processes were dependent upon and in turn affected various edaphic factors. Site replicates represent sampling over the growing season. Together, the x and y axes accounted for 91% ( $P < 0.1\%$ ) of the community variability. An ordination of the 1977 data gave a similar spatial arrangement with more vertical dispersion and the axes accounted for only 78% of the community variability. The greater vertical dispersion in the 1977 ordination may have been related to the increased rainfall, improved soil moisture conditions, and increased plant cover.

Figure 7. Ordination of the 1976 community replicates for Sites I, II, III, and IV in a portion of the Carberry Sand Hills.





Dune and intermediate communities are arranged linearly along the x axis with little vertical displacement while prairie replicates have greater spread. Since bare ground was used as a factor in determining the similarity indices, Sites I, II and III reflect its large percentage in their total cover. Site IV has considerably more plant cover, more species, and internal seasonal variability in species behavior than the preceding communities accounting for its greater dispersion and distance from them. There are no overlaps between adjacent communities and they maintain distinct groups while forming a continuum along the x axis and the factors it represents.

A linear regression of community replicate positions on the axes with mean values for edaphic factors at the surface and 40 to 60 cm depth indicated highly significant ( $P < 0.1\%$ ) correlations with the x axis, but not the y axis. Correlation coefficients were found to be .79 (surface) and .92 (40.60 cm) for pH; -.92 and -.81 for organic matter; -.78 and -.90 for conductivity and -.90 and -.93 for nitrogen. Phosphorus, potassium and soil texture were poorly correlated at either depth. Thus, the spatial distribution of communities follows gradients in soil characteristics. It appears that organic matter in surface layers and nitrogen to a depth of 40 to 60 cm are governing factors with pH and conductivity at 40 to 60 cm only slightly less important. Factors associated with dispersion along the y axis were not discernible from data obtained in the study and it is hypothesized that the y axis may be related to seasonal variability and changing species composition.

Vegetation Study. An analysis of vegetation data indicated a rapid increase in both complexity and richness during successive stages of colonisation. The 122 species found in the study area are listed in Table 2 with their average prominence values in the communities. Approximately 10% were infrequent or ruderal. Seventy-nine species were found in only one of the four sites. Twenty-four species were found in two or three adjacent sites, and only one, Andropogon gerardi, was found in all four sites. The colonisation process from dune to prairie was marked by an approximate doubling of species numbers with each successive stage that was recognized; from 9 species in Site I, to 17 species in Site II, to 34 species in Site III, to 77 species in Site IV.

Almost all species encountered were perennials and depended primarily upon vegetative reproduction to expand into new areas. Notable exceptions were two dune species. Helianthus petiolaris, an annual, depended upon successful seed dispersal and subsequent germination to ensure survival, and Oryzopsis hymenoides, a perennial, produced many seedlings, of which few survived to increase vegetatively.

Prominence values change throughout the growing season influenced by the phenology of individual species. Simplified phenophases for dominant species (Fig. 8) assist in interpreting the prominence value data (Figs. 9-12). Two growth strategies were observed. First was a unimodal increase in prominence where the maximum PV attained corresponded closely with the time of flowering. Oryzopsis hymenoides, Helianthus petiolaris,

Table 2. Average prominence values (PV) (cover  $\sqrt{\text{frequency}}$ ) for species in the study sites I-IV in the Carberry Sand Hills. A, B, and P refer to annual, biennial, or perennial respectively; and R denotes species which are predominantly ruderal. T indicates a PV less than 1.

Species	Site I	Site II	Site III	Site IV
<i>Corispermum simplicissimum</i> , A	6.3	-	-	-
<i>Oryzopsis hymenoides</i> , P	3.7	-	-	-
<i>Helianthus petiolaris</i> , A	3.6	-	-	-
<i>Rumex venosus</i> , P	T	-	-	-
<i>Andropogon gerardi</i> , P	1.2	49.4	28.5	T
<i>Elymus canadensis</i> , P,R	T	-	-	-
<i>Sporobolus cryptandrus</i> , P	T	-	-	-
<i>Salix interior</i> , P	T	-	-	-
<i>Lygodesmia juncea</i> , P	T	1.0	1.7	-
<i>Koeleria cristata</i> , P	-	77.6	41.8	-
<i>Petalostemum candidum</i> , P	-	32.8	T	-
<i>Artemisia campestris</i> ssp. <i>caudata</i> , P	-	20.7	11.5	2.7
<i>Solidago nemoralis</i> var. <i>decemflora</i> , P	-	8.1	25.2	-
<i>Elaeagnus commutata</i> , P	-	6.0	1.4	-
<i>Chrysopsis villosa</i> , P	-	1.9	T	T
<i>Bouteloua curtipendula</i> , P	-	1.3	1.3	5.9
<i>Lesquerella ludoviciana</i> , P	-	T	-	-
<i>Melilotus alba</i> , A,B,R	-	T	-	-
<i>M. officinalis</i> , A,B,R	-	T	-	-
<i>Grindelia squarrosa</i> , B,P	-	T	-	-
<i>Senecio canus</i> , P	-	T	-	-
<i>Townsendia exscapa</i> , P	-	T	-	-

Table 2. continued

Andropogon scoparius, P	-	T	38.3	15.0
Linum sulcatum, A	-	T	T	T
Tortula ruralis	-	-	3.7	-
Equisetum hyemale var. affine, P	-	-	T	-
Populus deltoides, P	-	-	T	-
Oxytropis lambertii, P	-	-	T	-
Rhus radicans var. rydbergii,	-	-	T	-
Mamillaria vivipara, P	-	-	T	-
Oenothera biennis, B,R	-	-	T	-
O. nuttallii, P	-	-	T	-
Cetraria islandica	-	-	T	-
Juniperus horizontalis, P	-	-	31.6	57.6
Calamovilfa longifolia, P	-	-	13.8	1.3
Festuca ovina, P	-	-	4.7	1.9
Carex spp. including: C. filifolia, P C. siccata, P C. stenophylla var. enervis, P	-	-	2.4	47.1
Juniperus communis, P	-	-	1.2	T
Poa palustris, P	-	-	T	T
Stipa spartea, P	-	-	T	45.5
Bouteloua gracilis, P	-	-	T	34.7
Rosa arkansana, P	-	-	T	4.2
R. blanda, P	-	-	T	T
Prunus virginiana, P,R	-	-	T	T
Petalostemum purpureum, P	-	-	T	4.7
Cladonia spp. including: C. cristatella C. pyxidata var. pocillum	-	-	-	45.5
Selaginella rupestris, P	-	-	-	11.9
Artemisia frigida, P	-	-	-	7.9
Lithospermum canescens, P	-	-	-	7.8
Mosses, considered collectively*	-	-	-	7.2

Table 2. continued

<i>Helianthus laetiflorus</i>				
var. <i>subrhomboides</i> , P	-	-	-	6.9
<i>Prunus pumila</i> , P	-	-	-	3.5
<i>Arctostaphylos uva-ursi</i> , P	-	-	-	3.4
<i>Artemisia ludoviciana</i>				
var. <i>gnapholodes</i> , P	-	-	-	2.4
<i>Aster pansus</i> , P	-	-	-	2.1
<i>Antennaria neodioica</i> , P	-	-	-	1.5
<i>Cerastium vulgatum</i> , P	-	-	-	1.2
<i>Heuchera richardsonii</i> , P	-	-	-	1.1
<i>Picea glauca</i> , P	-	-	-	T
<i>Poa compressa</i> , P	-	-	-	T
<i>Muhlenbergia cuspidata</i> , P	-	-	-	T
<i>Panicum wilcoxianum</i> , P	-	-	-	T
<i>Allium stellatum</i> , P	-	-	-	T
<i>Lilium philadelphicum</i>				
var. <i>andinum</i>	-	-	-	T
<i>Populus tremuloides</i> , P	-	-	-	T
<i>Comandra richardsiana</i> , P	-	-	-	T
<i>Chenopodium album</i> , A,R	-	-	-	T
<i>Mirabilis nyctaginea</i> , P	-	-	-	T
<i>Ranunculus rhomboideus</i> , P	-	-	-	T
<i>Anemone cylindrica</i> , P	-	-	-	T
<i>A. multifida</i> , P	-	-	-	T
<i>A. patens</i>				
var. <i>wolfgangiana</i> , P	-	-	-	T
<i>Arabis holboellii</i>				
var. <i>retrofracta</i> , B,P	-	-	-	T
<i>Amelanchier alnifolia</i> , P	-	-	-	T
<i>Fragaria virginiana</i> , P	-	-	-	T
<i>Chamaerhodos erecta</i>				
ssp. <i>nuttallii</i> , P	-	-	-	T
<i>Potentilla arguta</i> , P	-	-	-	T
<i>P. pensylvanica</i> , P	-	-	-	T
<i>Geum triflorum</i> , P	-	-	-	T

Table 2. continued

<i>Psoralea esculenta</i> , P	-	-	-	T
<i>Polygala senega</i> , P	-	-	-	T
<i>Androsace septentrionalis</i> , A	-	-	-	T
<i>Asclepias viridiflora</i> var. <i>linearis</i> , P	-	-	-	T
<i>Lithospermum incisum</i> , P	-	-	-	T
<i>Moldavica parviflora</i> , A,B	-	-	-	T
<i>Monarda fistulosa</i> , P	-	-	-	T
<i>Penstemon gracilis</i> , P	-	-	-	T
<i>Galium septentrionale</i> , P	-	-	-	T
<i>Houstonia longifolia</i> , P	-	-	-	T
<i>Symphoricarpos albus</i> , P	-	-	-	T
<i>Linnaea borealis</i> var. <i>americana</i> , P	-	-	-	T
<i>Campanula rotundifolia</i> , P	-	-	-	T
<i>Liatris punctata</i> , P	-	-	-	T
<i>Aster laevis</i> , P	-	-	-	T
<i>A. ptarmicoides</i> , P	-	-	-	T
<i>Erigeron glabellus</i> , P,R	-	-	-	T
<i>Rudbeckia serotina</i> , P	-	-	-	T
<i>Gaillardia aristata</i> , P	-	-	-	T
<i>Achillea lanulosa</i> , P	-	-	-	T
<i>Lactuca pulchella</i> , P	-	-	-	T
<i>Peltigera rufescens</i>	-	-	-	T

Following are species found in disturbed areas, but not actually part of the communities studied:

*Bromus inermis*, P,R  
*Setaria viridis*, A,R  
*Cycloloma atriplicifolium*, A,R  
*Salsola kali* var. *tenuifolia* A,R  
*Portulaca oleracea*, A,R  
*Corydalis aurea*, A,B,R  
*Lepidium densiflorum*, A,B,R

Table 2. continued

Erysimum asperum, P,R  
E. inconspicuum, P,R  
Prunus pensylvanica, P,R  
Euphorbia serpyllifolia, A,R  
Erigeron asper, P,R  
E. strigosus, A,B,R  
Senecio pauperculus, P,R  
Tragopogon pratensis, B,P,R

\*These included: Bryum spp., Ceratodon purpureus, and Tortula ruralis.



Corispermum simplicissimum, Andropogon gerardi, Artemisia campestris, A. frigida, and Helianthus laetiflorus (Figs. 9-12) follow this pattern. A second phenological pattern, of flowering followed by a quiescent period and late season vegetative reproduction, gave a bimodal curve to seasonal prominence values. This was observed in Lithospermum canescens, Koeleria cristata, Stipa spartea, Petalostemum candidum, and Andropogon scoparius (Figs. 10-12). Irregularities in the curves are caused, in part, by varying degrees of non-random species distribution in the field. The Caladonias (Fig. 12), for example, tend to grow in large scattered patches, rather than being evenly distributed; this produces an irregular PV curve. The possibility that other species exhibit a similar distribution must be considered when interpreting the prominence value graphs.

Two features are evident in the prominence values for bare ground (Fig. 13). First, PVs for bare ground are lower as colonisation progresses from Sites I to IV. Second, greater rainfall and soil moisture in 1977 resulted in lower values than 1976. A rise in values at week 13 of the first year reflected the dry conditions which caused early dormancy and decreased cover values for those plant portions still growing.

Initial colonisation is dependent upon seedling survival and vegetative reproduction. In Site I in 1976, Helianthus petiolaris increased to a maximum PV at its time of flowering (Fig. 9 ). Its low values during the second year were due to heavy mortality early in the season, when seedlings were undermined by strong winds before their roots were deep enough to

Figure 8. Phenophases of dominant species found in the Carberry Sand Hills, commencing with week 0, May 14-16.

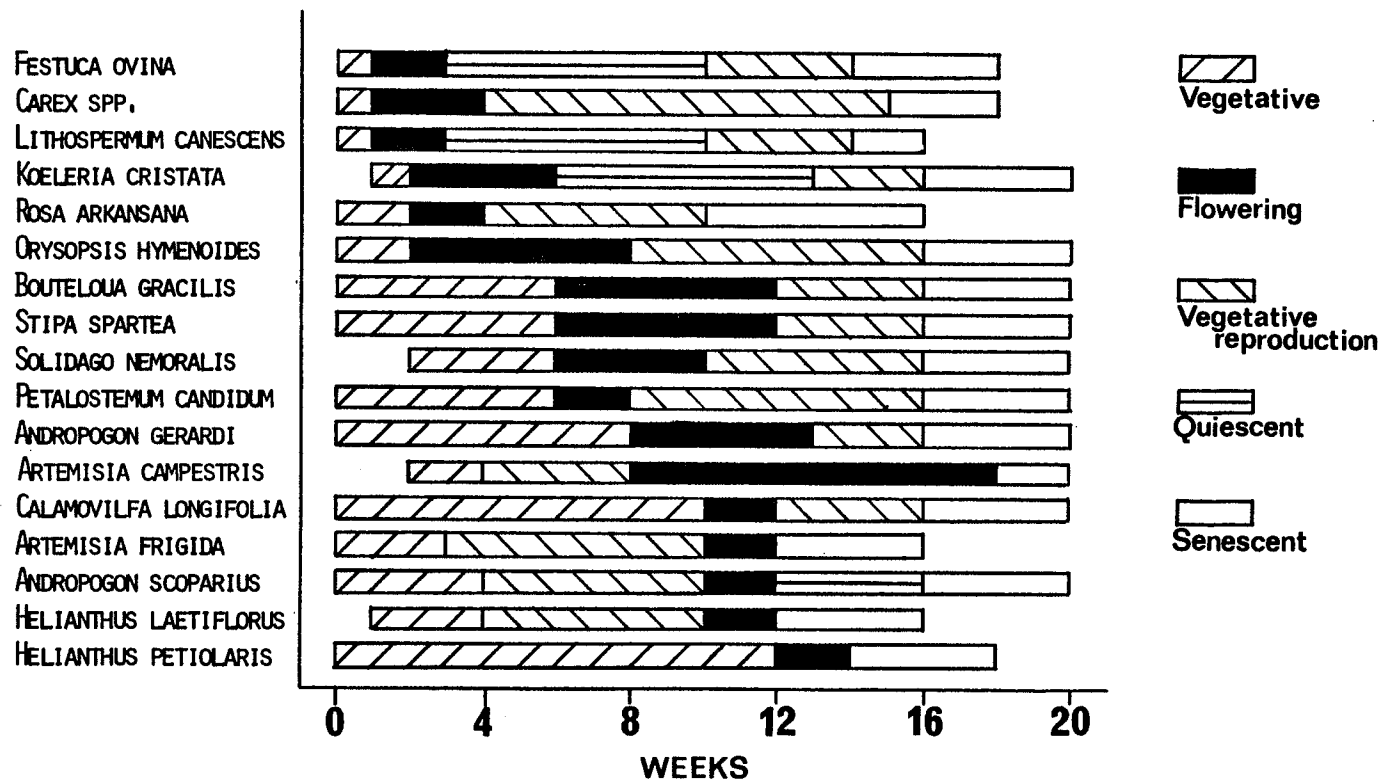


Figure 9. Prominence values for dominant species on Site I in the Carberry Sand Hills, where a is 1976 and a' is 1977. Week 0 commenced May 14-16.

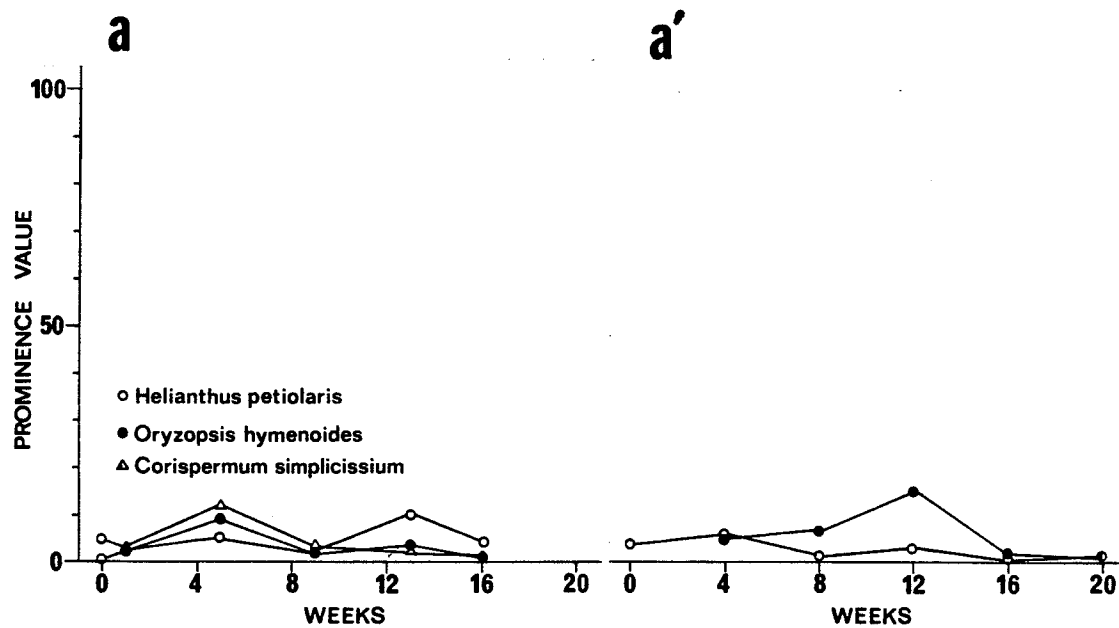


Figure 10. Prominence values for dominant species on Site II in the Carberry Sand Hills, where a is 1976 and a' is 1977. Week 0 commenced May 14-16.

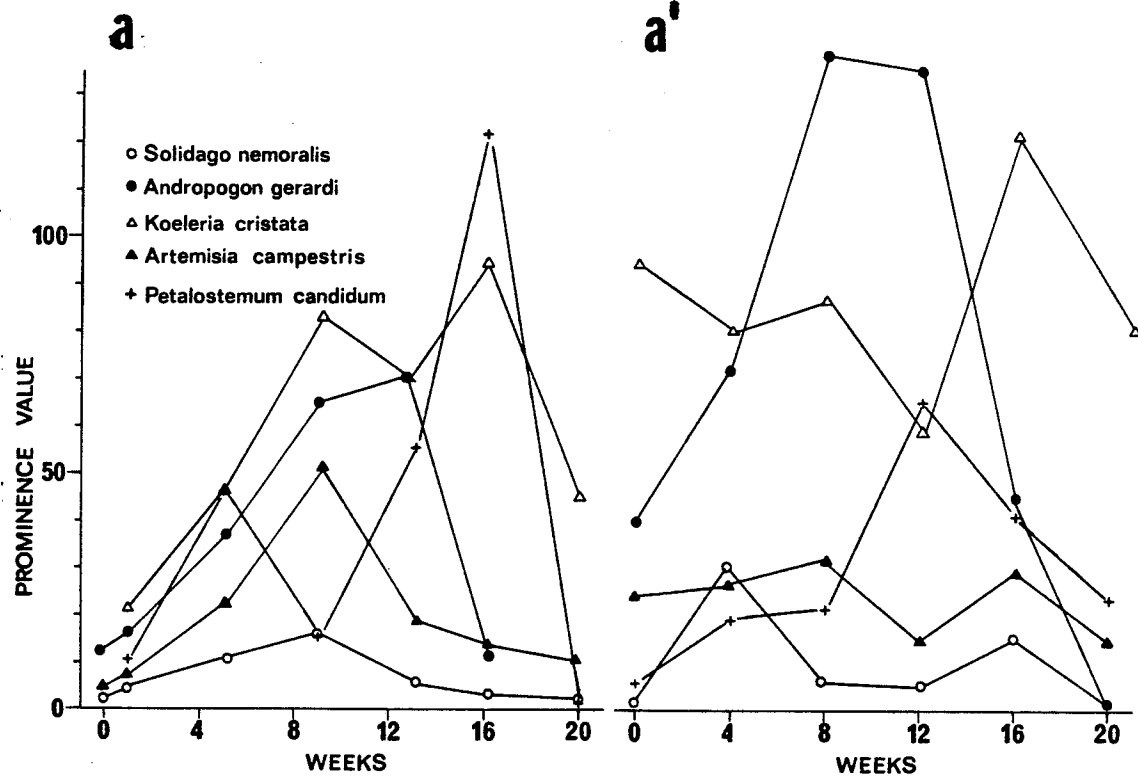


Figure 11. Prominence values for dominant species on Site III in the Carberry Sand Hills, where a, b are 1976 and a', b' are 1977. Week 0 commenced May 14-16.



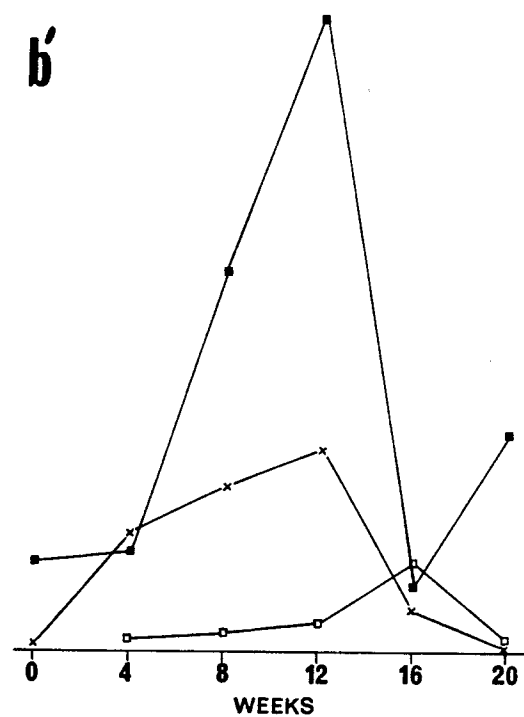
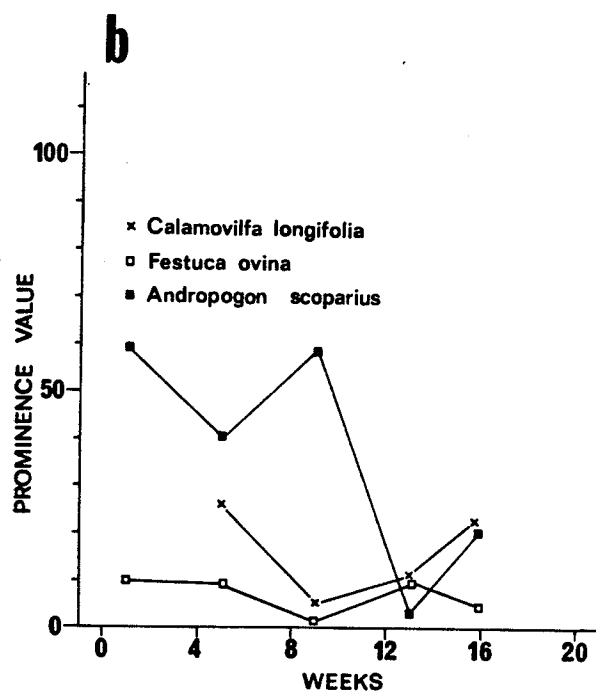
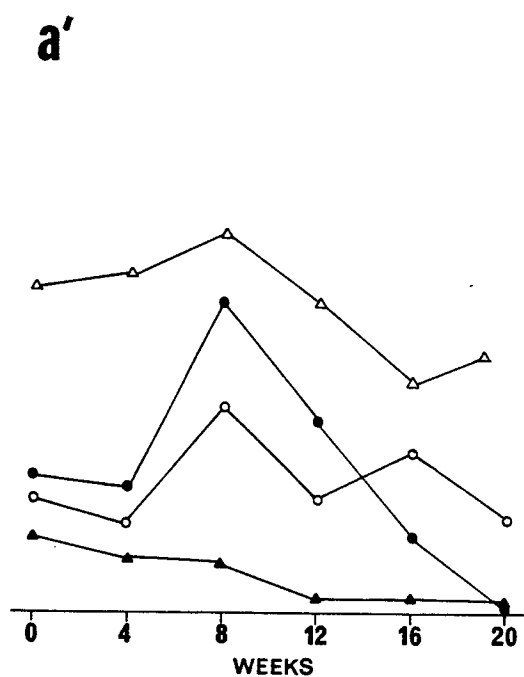
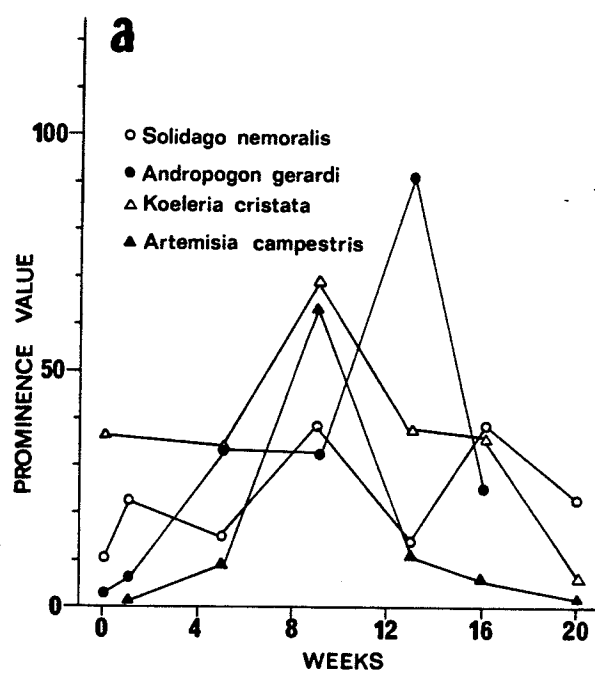


Figure 12. Prominence values for dominant species on Site IV in the Carberry Sand Hills, where a, b, c are 1976 and a', b', c' are 1977. Week 0 commenced May 14-16.

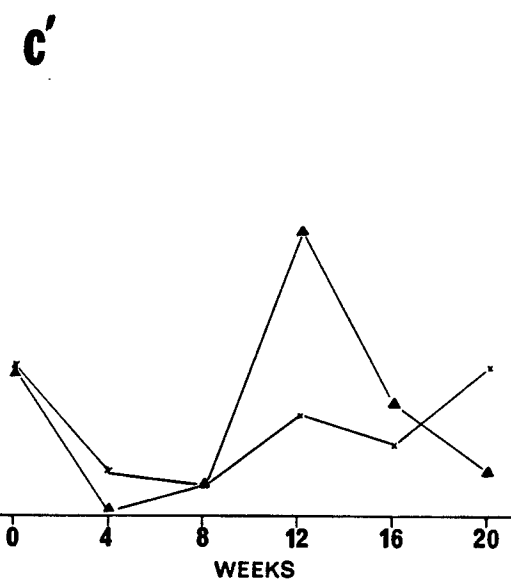
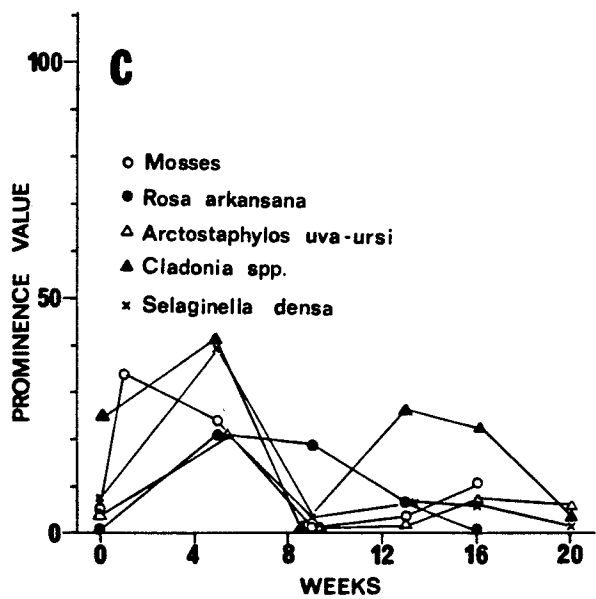
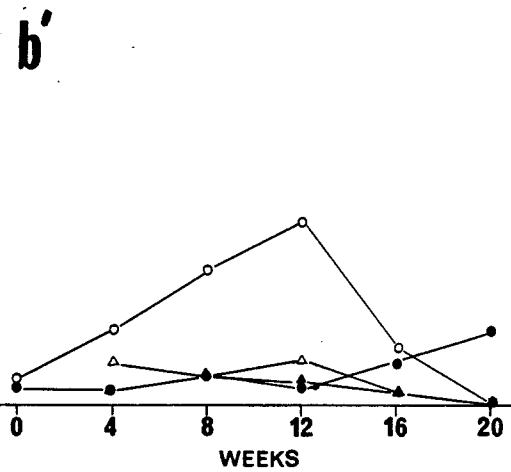
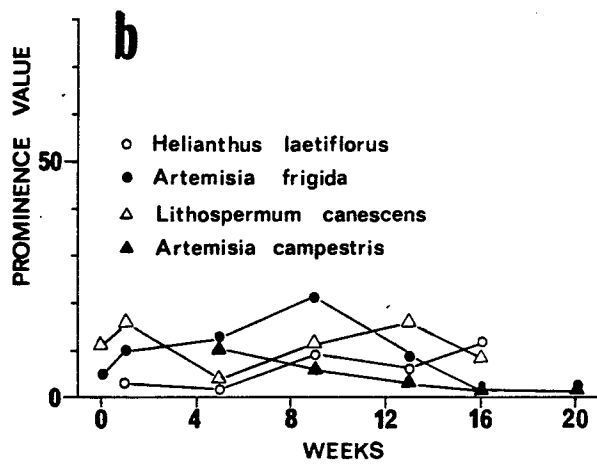
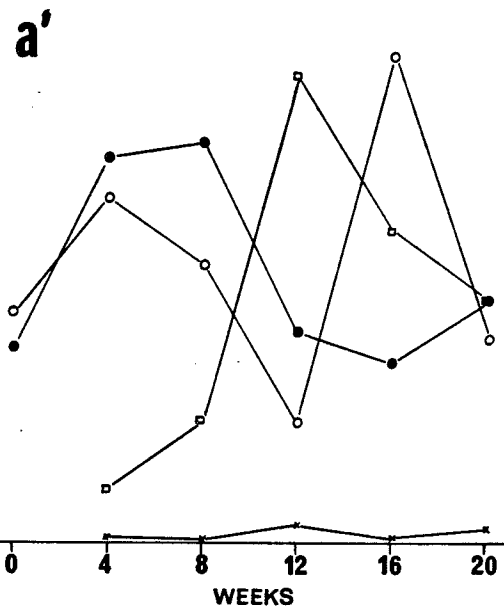
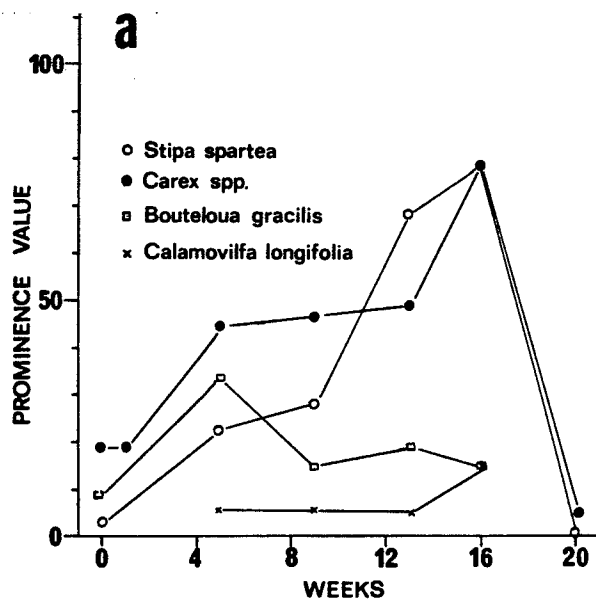
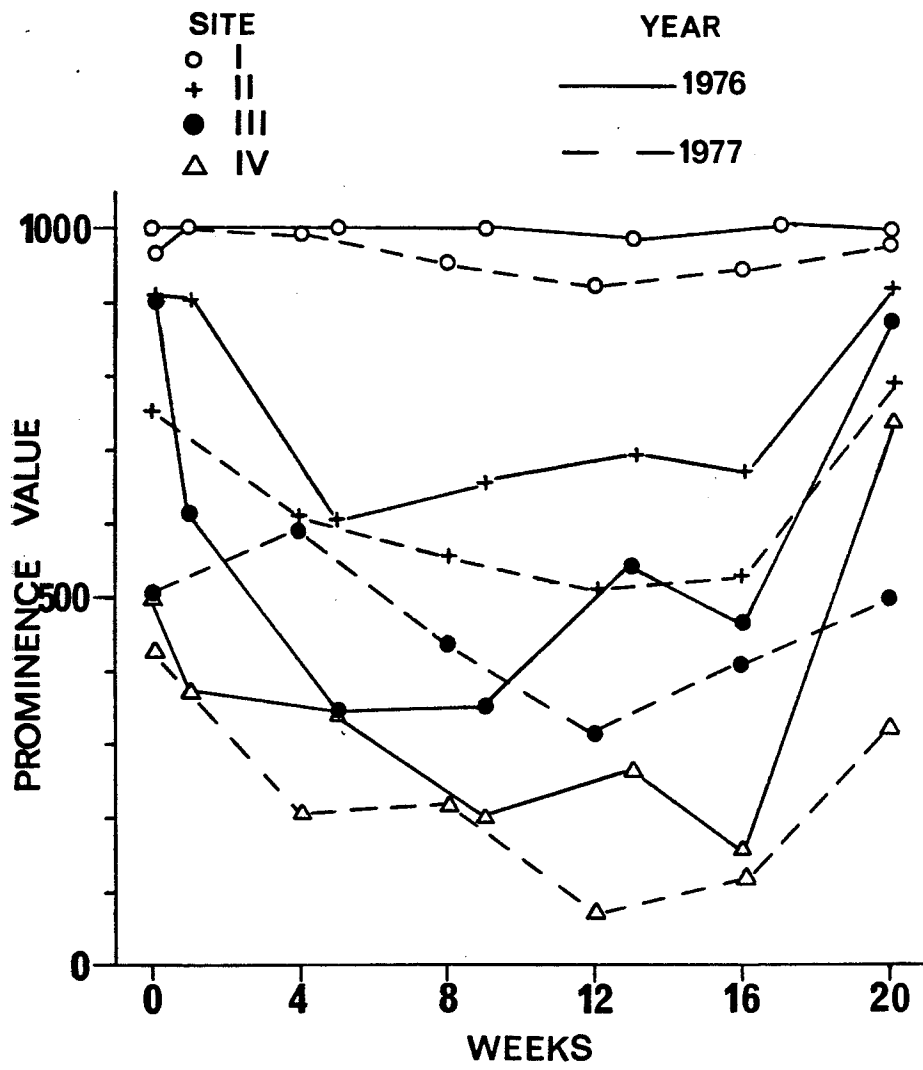


Figure 13. Prominence values for bare ground in 1976 and 1977. Week 0 commenced May 14-16.



provide sufficient anchorage. Oryzopsis hymenoides had a greater prominence the second year primarily through vegetative increase. Corispermum simplicissimum attained a maximum PV of 12 the first year but probably because of poor seed set or viability due to dry conditions, no plants were found the second year. Andropogon gerardi was common to Sites I and II and showed a marked increase in the latter.

Site II was dominated by the species shown in Fig. 10. In 1976, Andropogon gerardi and Koeleria cristata attained similar values. The former exhibited the unimodal increase at flowering time and the latter the bimodal pattern of late vegetative reproduction. Growth patterns for the two grasses were similar the following year but the PV's attained were about 30% greater, reflecting improved moisture conditions. In contrast the PV of Petalostemum candidum under dry conditions was twice that realized with above normal rainfall. The bimodal pattern one year and unimodal the next may have been due to sampling error or its spatial distribution. Artemisia campestris also attained a higher PV the first year with a peak corresponding with its flowering period. Its higher values in 1976, with lower than average precipitation, indicate its ability to grow in dry conditions. Solidago nemoralis had a PV six times as great the second year and exhibited a similar behavior pattern both years.

In Site III (Fig. 10) Andropogon gerardi and Koeleria cristata were less important than in Site II and were co-dominant with Andropogon scoparius. Festuca ovina, an early

flowering species, declined the first year when it became dry, and resumed vegetative growth in response to late rains. With sufficient moisture the second year, it showed a steady increase in vegetative growth. Calamovilfa longifolia flowers in mid-season. It increased slightly the first year after flowering, but had a progressive increase the second year. The fact that the phenological responses of F. ovina and C. longifolia varied between a dry year and a wetter than normal year indicates they were probably opportunistic.

Site IV was dominated by Juniperus horizontalis, Stipa spartea and three species of Carex. Because J. horizontalis has a patchy distribution but covers relatively large areas where it is found, its PVs varied widely and are not presented in graph form. Stipa spartea and Carex spp. (Fig. 12) bloom in late spring or early summer and reproduce vegetatively in late summer. In 1976 they had similar development patterns of increasing prominence until killed by frost in early September. The following year they declined at mid-summer coincident with a rapid increase in Bouteloua gracilis. S. spartea and Carex spp. then had divergent patterns for the remainder of the season. Bouteloua gracilis bloomed from weeks 6 to 12 which correlated with its prominence peak the second year. Its performance the first year, however, suggests that it may have been unable to compete with other species in dry conditions. However, Coupland and Johnson (1965) found Bouteloua gracilis to be drought resistant. C. longifolia was widely scattered on

the prairie and was a small contributor to this community compared with its role in Site III.

Artemisia frigida and Lithospermum canescens both reached a higher PV the first year than the second. The bimodal pattern of L. canescens reflects its early flowering reproduction by divisions of the crown, late in the season. Helianthus laetiflorus bloomed around week 12 at its maximum PV the second year; however, growth and flowering were delayed and sporadic the first year.

Artemisia campestris, a pioneer species, had progressively smaller PVs and reduced size and vigor of individual plants from Site II and IV. It was found in small disturbed areas on the prairie where its existence appeared marginal. Its decrease over the two year period indicates that it may disappear from the community should favorable conditions for other species continue.

Ground layer vegetation included Selaginella densa, several species of Cladonia, and mosses (Table 2). All grew well in early 1976 but declined in prominence late in the season. In the subsequent year, S. densa, with a maximum root depth of 5 cm (Coupland and Johnson, 1965) increased steadily, aided by more favorable moisture conditions in the surface soil. Cladonia spp. attained a maximum PV of 63 by week 12 of the second year, but were not observed as often thereafter, possibly because they became buried in litter or were overgrown by other species. Although the mosses had a PV of 44 in early 1976, they were rarely observed the



second year perhaps for similar reasons.

The increase in community complexity from Site I to Site IV was coupled with a concomitant increase in species-environment interactions. This was manifested by a greater range of plant statures and flowering periods that maximised the use of resources such as light, moisture, and nutrients. In Site I, Oryzopsis hymenoides and Helianthus petiolaris had different phenological patterns but had the same prominence. They comprised a small part of the dune cover and grew in slightly different areas. There was a large amount of bare ground between the widely spaced plants on Site II, but sufficient competition for nutrients and water occurred that the successful species had varied phenologies. Solidago nemoralis and Koeleria cristata, both short plants, reached their maximum growth before Andropogon gerardi attained its maximum height and they declined at the peak of prominence of A. gerardi. K. cristata and P. candidum have shallow-spreading, and deep taproot systems respectively, thereby avoiding competition for the same moisture sources.

In Site III, Andropogon scoparius reached twice the height of Festuca ovina and they had an inverse prominence relationship with Festuca blooming six weeks earlier. Likewise, plants of similar stature such as Koeleria and Solidago had staggered periods of flowering with Koeleria blooming before Solidago. Both were setting seed as they were overtopped by Calamovilfa longifolia and Andropogon gerardi.

Competition for light and moisture on the prairie is

more severe than in other sites as vegetation is much denser with little bare ground. Lithospermum canescens and other plants such as L. incisum, Geum triflorum and Anemone patens, flower early in the year before they are shaded by taller species. Carex spp. are low in stature, bloom early in the spring and begin their vegetative reproduction before Stipa spartea reaches its maximum development.

In summary, successional processes on the Carberry Sand Hills are marked by an increase in species cover, species diversity, and complexity of community structure proceeding from the bare dunes to the prairie. Four communities are recognizable on the basis of the community composition and topographic position. Plant cover increased from less than 1% on the dunes to about 70% on the prairie with an increase in species from nine on the bare dunes to 77 on the prairie. However, the communities are not distinct entities, but rather there are overlaps in species composition as micro-environmental effects are modified.

Colonization is accompanied by an increase in soil nutrients, organic matter and water retention but a decrease in pH. At the same time, greater plant cover is found with moderated temperature fluctuations at the soils surface and to depths of 30 cm. An analysis of edaphic factors also showed that communities varied along a continuum. As in most examples of primary succession, changes in species cover and richness, and environmental factors proceed together, thus making it difficult to elucidate their complex interactions.

### CHAPTER 3

#### TRAMPLING IMPACTS AND RECOVERY IN THE CARBERRY SAND HILLS

## METHODS AND MATERIALS

An experimental approach modeled after Cordes et al., (1975) and Shay and Shay (1979) was used to monitor the effects of trampling over a two year period in the four community types previously described. Trampling was conducted in 1976 and the ability to recover was observed in 1977. Plots 3x7 meters were established in each community on a level area with relatively homogeneous vegetation within the plots. Each plot contained seven lanes, 1x3 meters, to have 0, 10, 20, 40, 80, 160, and 320 tramples. A trample was defined as a one way walk through the lane and trampling was performed on a single day every other week, a total of eight times throughout the first year.

Before trampling began on June 5, 1976, each lane in all four plots was assessed for plant species cover and frequency by means of ten randomly placed 25x25 cm quadrats. As the season progressed it became apparent that attempting to assess the impacts from quadrat data was not practical. Therefore, a somewhat more qualitative approach was taken where the total amount of bare ground and species cover was assessed for each lane as a whole. Assessments were made at the beginning, middle, and end of both the trampling and recovery years. Permanent records were kept by photographing the lanes every four weeks during both years of the study.

## RESULTS

Cover values for bare ground and litter, and the dominant species for the trample plots before trampling began are given in Table 3. Species composition in Sites I and III had a high degree of internal similarity, while Sites II and IV exhibited a great deal of variability between lanes. In Site II, bare ground had a range of 39% to 78% in trample lanes 320 and 0 respectively. At the outset, therefore, the control lane had twice the amount of bare ground as the lane to receive the most severe impact. Lanes 40, 160 and 320 had three times as much Petalostemum candidum as the control. In Site IV, bare ground ranged from 18% to 47% although the control lane had a value of 28% which was relatively close to the mean value of 33% for the plot as a whole. Stipa spartea was not found in two lanes but had a maximum value of 14% in one lane. Carex spp. had a nine-fold variation between 4% and 36% cover while Bouteloua gracilis varied even more with a low of 2% and a maximum cover of 52%.

Results from the trampling season and recovery year for each community are presented below in note form.

## SITE I

Middle and end of trampling season. Site I had so little vegetation initially that it was not possible to distinguish between the effects at the middle and end of the trampling season. Therefore, these were combined for ease of presentation.

Table 3. Pre-trampling cover values for the dominant species in the Carberry Sand Hills, where cover is expressed as a percentage. Data was collected on June 5, 1976 using 10 quadrats 25 x 25 cm per lane.

Species	Number of tramples per lane						
	0	10	20	40	80	160	320
Site I							
Bare ground	96	97	95	90	97	96	94
<u>Lygodesmia juncea</u>	2	-	2	8	-	-	4
<u>Helianthus petiolaris</u>	1	2	2	1	2	2	2
Grass seedlings	1	1	1	1	1	2	-
Site II							
Bare ground	78	64	60	58	68	49	39
<u>Petalostemum candidum</u>	7	15	17	21	7	19	19
<u>Koeleria cristata</u>	10	12	14	10	9	20	12
<u>Andropogon gerardi</u>	3	1	1	2	3	2	2
Site III							
Bare ground	71	56	73	78	64	70	70
<u>Koeleria cristata</u>	6	2	9	4	16	5	2
<u>Andropogon gerardi</u>	14	13	12	11	15	11	12
<u>Solidago nemoralis</u>	4	2	4	4	3	2	7
Site IV							
Bare ground	28	40	47	36	30	18	36
<u>Carex</u> spp.	18	36	24	22	23	4	13
<u>Stipa spartea</u>	10	7	14	12	0	0	8
<u>Bouteloua gracilis</u>	13	2	2	15	24	52	26
<u>Artemisia frigida</u>	11	8	7	6	12	9	11

Control Lane. Bare ground had a cover value of 98% with the remainder of the cover being accounted for by about 30 Oryzopsis hymenoides seedlings and an equal number of Helianthus petiolaris.

10 Tramples. No damage was evident and the lane appeared equivalent to the control. H. petiolaris vigor and flowering were unimpaired.

20 Tramples. The O. hymenoides seedlings were reduced slightly in size and number and there was a faint path discernible if the center tread was compared to the margins of the lane.

40 Tramples. The center tread was completely bare of rooted plants and the H. petiolaris cover in the margins was about one half that found in the control plot. One well developed Lygodesmia juncea was rooted in the margins and overhung the center tread but appeared unharmed as it pivoted on its stem and was brushed aside.

80 to 320 Tramples. There was no plant growth in the treads and a progressive decline in the size and vigor of O. hymenoides and H. petiolaris was noticeable in the margins of the lanes. With 80 tramples a definite depression in the sand was noticeable. The tread became progressively deeper in the 160 and 320 lanes.

Beginning of the recovery year.

Control Lane. O. hymenoides seedlings doubled their size since the first year. Only 7 H. petiolaris seedlings were found this year.

10 Tramples. O. hymenoides seedlings were fewer and slightly smaller than in the control lane. No H. petiolaris seedlings were present.

20 Tramples. This lane appeared the same as the 10 lane.

40 Tramples. No new growth occurred in the center tread which was still completely bare. The L. juncea on the margin appeared healthy.

80 Tramples. Small clumps of two to three stems of O. hymenoides grew on the margins. The center tread was 100% bare.

160 and 320 Tramples. No growth occurred in the lanes.  
Mid-recovery year.

Control Lane. O. hymenoides matured and flowered and the number of H. petiolaris increased to 16.

10 Tramples. The same general number of plants was found as in the control but their size had been reduced to about two-thirds of normal.

20 Tramples. O. hymenoides failed to flower and there were four H. petiolaris seedlings.

40 to 320 Tramples. Bare ground was 100%. No recovery was evident and these lanes appeared the same as at the beginning of the year.

End of recovery year. No further changes from those described for the mid-season assessment were observed. Even after a full year with no trampling it was still possible to observe a physical depression in the sand levels for



the 160 and 320 lanes in spite of the erosion of the margins and fill-in of the tread caused by wind blown sand.

An assessment of vulnerability and ability to recover is difficult on the open dunes, as there is very little vegetation present to be affected. It appears however, that 20 tramples in the first year left a visible impression on the plants. An effect from 10 tramples was not apparent the first year but caused a reduction in plant numbers and size in the recovery year.

#### SITE II

##### Mid-tramplng season.

Control Lane. Increased plant growth since spring reduced the amount of bare ground and litter to about 60%.

10 Tramples. No difference was observed between this and the control lane.

20 Tramples. A slight tread was discernible caused primarily by the removal of dead Andropogon gerardi stalks and other standing litter.

40 Tramples. A path was definitely observable due to an absence of litter and matting of the Koeleria cristata in the tread. Petalostemum candidum growing in the margins was very vigorous, flowered well, and overhung the tread, partially concealing the bare ground.

80 Tramples. Bare ground and litter accounted for 75% of the area but this lane had a high percentage of bare ground from the outset.

160 Tramples. Bare ground and litter accounted for 50% of the area but this lane had twice the amount of K. cristata and almost three times as much P. candidum as the 80 lane. About half of the bare ground had lost its litter cover.

320 Tramples. Bare ground accounted for 75% of the tread area. At least half of this no longer had any litter cover and the soil surface was becoming worn. Soil integrity maintained by the root systems broke down in over half the tread area leaving loose sand. Only the K. cristata survived in the tread itself with P. candidum being maintained on the margins and overhanging the tread.

End of the trampling season.

Control and 10 Tramples. No change from the mid-season assessment was observed.

20 and 40 Tramples. Both lanes had 50% bare ground in the tread with good vegetation growth in the margins.

80 Tramples. Bare ground increased slightly from the mid-season assessment to about 80%. However, the bare ground lost its previous litter cover and became loose and unconsolidated in some small areas.

160 Tramples. Bare ground increased to 90% with the death of the K. cristata. Grass clumps maintained the soil integrity in their immediate vicinity. However, about 80% of the bare ground was loose and unconsolidated.

320 Tramples. No plants were found in the tread and the totally bare soil had become loose and unconsolidated

to a depth of about 5 cm.

Beginning of recover year.

Control Lane. Fifty percent of the area was bare ground. K. cristata formed clumps up to 20 cm diameter although most were about 10 cm. P. candidum and Andropogon gerardi exhibited good growth and there were a few Artemisia campestris and Solidago nemoralis.

10 Tramples. P. candidum was only half as large as in the control lane and the K. cristata clumps were still flattened and broken into smaller remnants about 5 cm in diameter. Andropogon gerardi provided half the cover in the control lane but this reflected the original composition of the lanes before trampling began. This lane also had a few A. campestris and S. nemoralis.

20 Tramples. Bare ground covered about 70% of the total area in the tread and only small remnants of K. cristata were observed. P. candidum was half the size of that in the control and no A. gerardi was present in the tread or margins.

40 Tramples. Fifty percent of the center tread was bare ground. P. candidum in the margins had vigorous growth and overhung the center of the path making it appear less damaged than in the 20 lane.

80 Tramples. Bare ground accounted for 95% of the tread area with the remaining 5% covered by one small clump of K. cristata and a few clumps of S. nemoralis.

160 Tramples. Bare ground was the same as in the 80 lane. P. candidum on the margins were about one quarter

the size of those found in the control lane. Four new Lygodesmia juncea were found along with two shoots of Andropogon gerardi.

320 Tramples. The tread was 100% bare ground with no covering litter and sparse growth on the margins.  
Mid-recovery year.

Control and 10 Tramples. Plant cover in both lanes increased to 75% and no difference in the tread was discernable.

20 Tramples. Bare ground accounted for 40% of the center of the lane. The tread was noticeable although it was still covered with litter. P. candidum rooted in the tread covered most of the center portions of the tread. A few small clumps of K. cristata were also found.

40 Tramples. Plants appeared much more vigorous here than on the 20 lane and P. candidum had a denser growth. The bare ground was devoid of litter and was reduced to 25% of the tread area.

80 Tramples. Bare ground accounted for 75% of the area in the tread and there was no litter. Two P. candidum and S. nemoralis, and six small clumps of K. cristata were growing in the tread.

160 Tramples. The tread was 80% bare ground but a vigorous growth of new and older P. candidum overhung the path and made it appear as if there was more vegetation than in the 80 lane.

320 Tramples. This lane was similar to the 160 lane

situation where a vigorous growth of P. candidum on the margins made it appear that some regeneration had occurred in the tread although it was still 95% bare ground.

End of recovery year. No changes in the amount of cover were detected from the middle of the recovery year in the control, 10, 20, and 40 lanes. However, there was a 5 to 10% reduction in the amount of bare ground in the 80, 160, and 320 lanes caused by the germination and development of young P. candidum seedlings. Some seedlings attained a height of 8 cm before being killed by frost.

Increased trampling pressure was first observed by the removal of standing litter which occurred by mid-season with 20 tramples. This was followed by a matting of Koeleria cristata in the 40 trample lane. Mid-season in the 320 lane was marked by a loss of litter on the soil surface and a loosening of soil structure. K. cristata was killed by the end of the year after 160 tramples and soil was unconsolidated in the 80 and 320 trample lanes. Recovery of the trampled vegetation consisted primarily of new growth from seedling establishment of Petalostemum candidum in the loose soil of the most severely damaged areas.

### SITE III

Some of the effects of trampling and the ability to recover can be seen in Figure 14.

Mid-trampling season.

Control and 10 Tramples. Both appeared the same and no evidence of trampling was observed.

20 Tramples. The tread was about 50% bare ground; a decrease from the pre-trampled condition brought about by spring growth. However, Andropogon gerardi was about half the size and cover as in the control and 10 lanes.

40 and 80 Tramples. These appeared the same as the 20 lane. In both cases the bare ground was still covered with litter.

160 Tramples. Bare ground increased to 90% and most of the litter was loosened and removed. No A. gerardi survived in the tread although it was only slightly impaired on the margins. Koeleria cristata was reduced in size in the tread but accounted for most of the 10% cover while Solidago nemoralis had 1 to 2% cover.

320 Tramples. The tread was 100% bare ground with no litter cover. K. cristata and A. gerardi grew only in the margins.

End of trampling season.

Control and 10 Tramples. There was no difference observed between the two lanes other than the internal variability present in the species composition in the pre-trampling assessment.

20 Tramples. A definite tread was observable, but its presence was marked more by the absence of standing litter and a slight matting of the remaining plants rather

Figure 14. Trample plots on Site III; a) control and 10 trample lanes at the end of the trampling season, b) 160 and 320 lanes at the end of the trampling season, c) 160 and 320 lanes at the beginning of the recovery year, d) 160 and 320 lanes in mid-recovery year.







than an increase in the amount of bare ground.

40 Tramples. Seventy percent of the tread was bare ground and plant cover was equally divided between K. cristata and S. nemoralis. The latter bloomed more profusely here than in the previous lanes.

80, 160, and 320 Tramples. No plants survived this degree of trampling and the lanes were marked by a total absence of litter and an increase in both width and depth of unconsolidated soil. Margins were progressively narrower, with a reduction in plant size and cover to about half that of the control and 10 lane.

Beginning of recovery year.

Control Lane. The clumps of K. cristata were 10 to 15 cm in diameter and good growth was exhibited by Artemisia campestris, Solidago nemoralis and Andropogon gerardi.

10 Tramples. Cover was about the same as in the control lane but there was no standing litter. K. cristata clumps were smaller, 4 to 6 cm in diameter, and their growth appeared slightly delayed. A. campestris and S. nemoralis grew well and appeared unaffected.

20 and 40 Tramples. The center tread was 50% bare ground. Some clumps of K. cristata were dead but not broken down while those that survived were slightly smaller than in the 10 lane. No new growth was developing in old A. gerardi tufts in the tread but new shoots were developing from rhizomes of the plants on the margins. A. campestris and S. nemoralis survived only in the margins.

80 Tramples. The center tread was 90% bare ground and no A. campestris or S. nemoralis were found in the lane. K. cristata survived only in small clumps at the margins. About a dozen shoots of A. gerardi were growing from rhizomes in the center of the tread.

160 Tramples. The center tread was 95% bare ground. New Andropogon gerardi shoots emerged between the center of the tread and the margins. A few S. nemoralis survived in margins.

320 Tramples. The whole lane was completely bare except for four shoots of A. gerardi and three 4 cm diameter clumps of Blouteloua curtipendula.

Mid-recovery year.

Control and 10 Tramples. Both lanes had normal growth and flowering of Andropogon gerardi, Koeleria cristata and Solidago nemoralis. No difference between the lanes was discernible.

20 and 40 Tramples. The tread was moderately observable and had about 75% bare ground, little different from the pre-trampling assessment. Mature A. gerardi failed to flower but produced a vigorous growth of new shoots in the tread.

80 and 160 Tramples. Both lanes had 90% bare ground in the center tread. The 80 lane had four small clumps of A. gerardi with only a few new shoots produced while the 160 lane had twice as much regeneration by new shoots.

320 Tramples. Bare ground accounted for 95% of the

tread area with the 5% plant cover provided by 3 new shoots of A. gerardi and about 15 young dicotyledon seedlings.

End of recovery year.

Control and 10 Tramples. As before, both lanes appeared identical.

20 Tramples. A slight path was still evident due to the loss of standing litter.

40, 80, and 160 Tramples. All these lanes were about 75% bare ground. The 40 lane was relatively little changed from the mid-summer assessment but the 80 and 160 showed a decrease in the amount of bare ground due to the new growth of Andropogon gerardi from rhizomes of parent plants in the lane margins.

320 Tramples. No recovery was evident as the tread was still bare except for a few A. gerardi shoots which did not progress beyond their mid-summer development. The dicotyledon seedlings failed to survive.

Trampling impacts were apparent by mid-season with the reduction in size and cover of Andropogon gerardi in the 20 trample lane. Increased trampling intensity caused a complete loss of A. gerardi although Koeleria cristata was more tolerant. After a season of moderate impact, 40 tramples every two weeks, S. nemoralis bloomed more profusely than in the control lane. In the recovery year, spring growth of K. cristata was delayed in the 10 trample lane. A. gerardi failed to flower in the 20 trample lane but its vegetative

reproduction from rhizomes was stimulated. Recovery from severe trampling in this community appeared to depend primarily upon rhizomes of A. gerardi invading exposed and disturbed soil.

#### SITE IV

Some of the effects of trampling and the ability to recover can be seen in Figure 15.

##### Mid-trampling season.

Control and 10 Tramples. No difference between the two lanes was observed.

20 Tramples. A slight path was observable due to the removal of standing litter and matting of the Carex spp. and grasses.

40 Tramples. Matting of the plants was more severe and high spots on the tread were beginning to show signs of abrasion and plant removal. Bare ground was about 40% of the tread area.

80 tramples. Bouteloua gracilis declined by about 50% and Carex spp. were severely matted.

160 Tramples. Bare ground increased to about 80% in the tread. All growth ceased and was flattened to the point of becoming broken and removed.

320 Tramples. Bare ground and litter accounted for 100% of the tread area. Most of this was still covered by litter although the high spots lost their litter cover and exposed the bare soil.

Figure 15. Trample plots on Site IV, a) control and 10 trample lanes at the end of the trampling season, b) 160 and 320 lanes at the end of the trampling season, c) 160 and 320 lanes at the beginning of the recovery year, d) 160 and 320 lanes in mid-recovery year.





End of trampling season.

Control Lane. Bare ground accounted for about 5% of the total surface area.

10 Tramples. A faint path was observable caused by the partial removal of standing litter and a slight matting of some plants. Bouteloua gracilis and Carex spp. were the most resistant to matting.

20 Tramples. A definite path was visible with more matting of the vegetation. Carex spp. were broken down to the ground level although the crown and roots had not lost their integrity.

40 Tramples. About 40% of the tread was bare ground and litter with some high spots worn through to the soil. Carex spp. and B. gracilis on the high areas were worn through to the exposed root stocks.

80 Tramples. Fifty percent of the tread was bare ground and litter. No Bouteloua gracilis survived in the tread. All the Carex spp. were worn down to the root stocks.

160 Tramples. All growth in the tread was completely flattened and dead leaving 100% bare ground and litter. About 20% of the area had worn through completely to the sand.

320 Tramples. Previous growth was removed leaving little litter in the tread. About 50% of the bare tread was worn through to the sand which was loose and unconsolidated in small areas.

Beginning of recovery year.

Control Lane. The control lane had a good growth of Artemisia frigida, Carex spp. and Bouteloua gracilis.

10 Tramples. The amount of cover and species vigor was the same as the control except for a noticeable breakage and thinning of the Carex spp.

20 Tramples. A definite tread was observable and no standing litter was left from the previous year. No Carex spp. were found in the tread although B. gracilis was unimpaired. Artemisia frigida was about half as tall as in the control lane.

40 Tramples. B. gracilis was still thriving in the tread. Although the Carex spp. had been broken down to the root stocks, new shoots emerged. Three 5 cm diameter patches of bare ground were worn through to the sand.

80 Tramples. The vegetation was the same as in the 40 lane but the bare spots were twice as large.

160 Tramples. Only B. gracilis had any new growth. No Carex spp. or A. campestris survived in the tread. The absence of Carex spp. probably reflected its low cover initially. Bare spots covered four times as much area as in the 40 lane.

320 Tramples. About 75% of the tread, or twice that in the 160 lane was bare ground. No B. gracilis was found in the tread although both B. gracilis and Carex spp. on the edges of the bare spots were growing vigorously.



End of recovery year.

Control, 10, and 20 Tramples. All three lanes appeared virtually the same.

40 Tramples. The tread was barely visible and was marked by a few slightly worn spots. Vegetation had the same appearance as the previous lanes.

80 Tramples. The tread was moderately visible and was noticeable by an absence of standing or surface litter and a more vigorous growth of Bouteloua gracilis than previous lanes.

160 and 320 Tramples. The tread was highly visible, but exposed soil in the bare spots was colonized by Funaria hygrometrica to a large extent. Vigorous growth of B. gracilis produced thicker clumps, twice the diameter of those in the control lane. Young Artemisia frigida plants reached a height of about 5 cm.

Trampling effects were first observed by a removal of standing litter and matting of the graminoids. Bouteloua gracilis and Carex spp. were the most resistant species however, and survived 40 tramples every second week for the entire trampling season. B. gracilis growing in the margins of heavily trampled lanes had an increased flower and tiller production. Exposed soil was colonized by mosses and Artemisia frigida seedlings.

## DISCUSSION

From the results it can be seen that 20 tramples every second week, (160 over the summer), on Sites I, II, and III, and 10 tramples (80 over the summer), on Site IV left a recognizable impact on the vegetation. At the end of the recovery season Site I had reduced plant size in the 10 trample lane. Sites II and III still had observable impacts in the 20 trample lanes and Site IV had a reduction in plant size in the 10 trample lane. Although different species were affected in the four sites, it appears that all successional stages were equally sensitive to trampling impacts. This observation is in direct conflict, however, with Liddle's (1975) theory that vegetation becomes more tolerant to trampling pressures as plant succession proceeds. Furthermore, recovery appeared to occur equally slowly in all four communities.

Numerous problems beset the data gathering and interpretation aspects of this study. Most could have been avoided if the community structures and species phenology had been known beforehand. At the outset, the community composition of each lane was determined by randomly placed 25x25 cm quadrats. As trampling progressed and a center tread without vegetation developed it became apparent that randomly placed quadrats would either record no vegetation at all, and thus fail to account for impacts on the margins, or they would record almost normal vegetation and distort the damage caused by trampling.

In the 320 trample lanes it soon became evident that the original definition of bare ground used in the community study to describe bare ground and litter, was unsatisfactory to describe the degrees of "bareness" caused by trampling. These proceeded from bare ground with litter, to bare ground with no litter, to bare ground which was consolidated by underlying root structures, to bare ground which had become loose and unconsolidated. For these reasons, a qualitative approach was adopted during late July 1976.

Mid-way through the trampling procedure several phenomena were noticed which were thought to support statements and descriptions in the literature. One of these was the observation of an apparent increase in size and vigor of Petalostemum candidum in the 40 trample lane of Site II. Several reports (Liddle, 1975; Cole, 1978) indicated moderate trampling had a stimulatory effect on some species, and that appeared to be the case with P. candidum. But, there was three times as much P. candidum in the 40 lane as the control. Furthermore, the 40 lane plants appeared older, and as perennials were therefore larger. Also, their surprising vigor in mid-season after a total of 160 tramples, coincided with their maximum development and flowering. From the data collected here it is not possible to know if P. candidum was indeed stimulated by moderate trampling or whether that interpretation was precipitated by an initially large local population and coincidental normal phenological development. The reverse situation was observed on Site IV

when Lithospermum canescens appeared to decline with progressive trampling. L. canescens normally has an early spring growth and development phase followed by a loss in size as it becomes dormant by mid-summer. Thus, its disappearance was initially linked with trampling pressure. This was compounded by the fact that it occurred with a higher frequency in the trample lanes than the control lane and its absence was more dramatic. Not until the season was over was its disappearance firmly linked with its normal phenological pattern rather than with trampling pressure.

It is possible that published research on trampling might also have involved similar distortions, but because the investigators have most often not indicated the frequency or timing of the vegetation assessments it is difficult to interpret their findings accurately in light of the difficulties encountered here. Only Shay and Shay (1979) mentioned the difficulties of phenological changes over a growing season, although they and others (Landals and Scotter, 1973) observed difficulties in obtaining homogeneous trample lanes. Differences in community composition of successive lanes were not initially anticipated here and underscore the need for sufficient community information to establish lanes large enough to insure uniform composition.

A final consideration in the trampling study is the validity of the approach itself. While it is convenient for the researcher to trample an area 40, 80, 160, or 320 times in a half hour period it in no way resembles the pattern of

normal recreation use where that number of hikers might be spread more or less evenly over a two week period. In spite of the fact that numerous researchers have adopted this method of study, little effort has been made to determine if it is ecologically or recreationally valid. Only Cieslinski and Wagar (1970) compared simulated trampling on plots receiving two passes of a roller three days a week with 12 passes of the roller once every second week. No difference was found, but the trampling was of such low intensity that no effect was noticeable at all. There is no reason to believe that 320 tramples in a half hour period which can totally destroy some species might not be tolerated if the trampling was evenly spaced over two weeks. Until this question has been answered, this and similar studies are of relatively little value in attempting to apply sound ecological research to land use and recreation management.

Future attempts to analyze the effects of human impact and trampling should attempt to avoid the inherent problems found in this study. First and foremost, research should be conducted to determine if the effects of numerous tramples in a short period of time are equivalent to the same number in a longer period. Such research would need to be undertaken in a variety of ecosystems and community types. If the method is not entirely valid and a controlled intensity trampling study is deemed desirable, then it should be modeled on the use patterns of historic and predicted recreation demands. Thus, an area far from a large urban centre might

have a fairly uniform daily visitor rate, since most visitors would be on extended trips and staying for one or more nights in the area. In contrast, parks or sites of interest close to urban areas have the greatest number of visitors and impact on weekends since they are easily accessible for weekend leisure time.

Second, it is imperative to have sufficient knowledge of the plant communities being studied to insure an adequate sample size. A trample area three meters long was clearly insufficient to insure homogeneity in the communities discussed here. For an adequate sample, fewer sampling intensities with lanes up to 20 meters long would probably be preferable. An alternative to collecting data by quadrats would be to use a line intercept method with one line placed in the center of the lane and another on or near the edge of each tread.

Finally, it is necessary to understand the normal phenological behavior of the species being trampled to avoid incorrect interpretations of their response to trampling. It is also important to realize that behavior may vary from year to year as illustrated by the earlier prominence value graphs. In this trampling effort, the trampling was carried out in a dry year and recovery took place in a year of above normal rainfall. It is, therefore, difficult to determine how much a species responded to insufficient moisture, trampling or a combination of the two. Likewise, recovery and regeneration may have been aided by improved moisture conditions

in the second year of the study.

This study indicated the Carberry Sand Hills were very sensitive to trampling impacts and slow to recover from the destruction of the vegetation. Highly sensitive areas such as dunes and sand hills require careful planning by recreation managers to insure the preservation of the ecosystem. Any form of intensive recreation in this ecosystem would rapidly cause its destruction. Its best value is probably for nature interpretation walks. As long as visitors are aware of their impact and are willing to stay on designated trails the beauty they seek will be relatively unimpaired.

## CONCLUDING COMMENTS

The research reported here addressed two aspects of the vegetation found in the Carberry Sand Hills. The first concerns the vegetative colonization and subsequent development of plant communities in a portion of the sand hills. Successional trends parallel those found elsewhere in similar situations and involve an increase in plant cover, species richness, and changes in soil characteristics. The second aspect of the study attempted to ascertain the ability of the area to withstand and recover from foot traffic associated with recreational activities. Results of trampling experiments show that successional stages are easily damaged and slow to recover. A number of the problems inherent in trampling experiments are also discussed. These problems will hopefully be overcome in future trampling studies.

Basic phenological data is not available for the majority of Manitoba species. Such information would be an asset in most ecological research and is a pre-requisite for effective trampling studies.

One research area beyond the scope of the present work is the investigation of the time scale involved in succession from bare sand to prairie. The aerial photographs presented earlier suggest that detailed study of a sequence of dunes would be valuable. Other photographic records, as well as maps and accounts coupled with radio carbon dating of buried soil horizons could provide a chronology for the dunes. The interaction of species at various stages in dune



succession and changes in pattern during community development are also poorly understood. Little is known of root stratification or of the importance of allelopathy in species interactions. Good candidates for allelopathic studies would be Andropogon gerardi, Artemisia spp. and Helianthus petiolaris. Autecological studies of the dominants such as Andropogon gerardi, Koeleria cristata and Artemisia campestris, would be valuable. Especially important would be investigation of the nutrient requirements and adaptive mechanisms.

Blowouts in all successional stages are evident throughout the Carberry Sand Hills, but it is not known whether recolonisation of such sites mirrors initial colonisation.

The present investigation focused upon vegetation changes. Minimal attention was paid to edaphic factors, but the soils merit a detailed study which could include nutrient availability, cation exchange capacity and the rate of decomposition of organic material.

Because these sandhills are unique landforms in Manitoba and support unusual plant communities, they are of interest to the general public. The presence of people in such fragile areas unavoidably has an impact. It should, however, be possible to design appropriate footpaths so that the landscape suffers minimal damage while allowing its recreational and interpretive potential to be realized. To achieve this goal adequate information relating to the

temporal and spatial aspects of dune succession is essential. Sandhills must be adequately understood before they can be successfully managed.

## LITERATURE CITED

- Albertson, F.W. 1941. Prairie studies in west central Kansas. Kan. Acad. Sci. Trans. 44: 48-57.
- Albertson, F.S. and J.E. Weaver. 1944. Effects of drought, dust, and intensity of grazing on cover and yield of short-grass pastures. Ecol. Monogr. 14: 1-29.
- Allen, S.E., A. Carlisle, E.J. White, and C.C. Evans. 1968. The plant nutrient content of rainwater. J. Ecol. 56: 497-504.
- Alvin, K.L. 1960. Observations on the lichen ecology of South Haven Peninsula, Studland Heath, Dorset. J. Ecol. 48: 331-339.
- Ayyad, M.A.G. and R.L. Dix. 1964. An analysis of a vegetation micro-environmental complex on prairie slopes in Saskatchewan. Ecol. Monogr. 34: 421-442.
- Bagnold, R.A. 1941. The Physics of Blown Sand and Desert Dunes. Wm. Morrow, New York, N.Y. 265 pp.
- Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks and gateways. J. Ecol. 23: 470-487.
- . 1938. Life forms of pasture plants in relation to treading. J. Ecol. 26: 452-454.
- Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bulletin 72: 156-181.
- Bird, R.D. 1927. A preliminary ecological survey of the district surrounding the entomological station at Treesbank, Manitoba. Ecology, 8: 207-220.
- . 1961. Ecology of the Aspen Parkland. Canadian Department of Agriculture, Research Branch. 155 pp.
- Birse, E.L. and G.H. Gimingham. 1955. Changes in the structure of bryophyte communities with the progress of succession on sand dunes. Trans. Brit. Bryol. Soc. 2: 523-531.
- Birse, E.M., S.Y. Landsberg and C.H. Gimingham. 1957. The effects of burial by sand on dune mosses. Trans. Brit. Bryol. Soc. 3: 285-301.
- Blom, C.W.M.P. 1976. Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes: I. Soil compaction, soil moisture and seedling emergence. Oecol. Plant. 11: 225-241.

- \_\_\_\_\_. 1977. Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes: II. Trampling and seedling establishment. *Oecol. Plant.* 12: 363-382.
- Boorman, L.A. and R.M. Fuller. 1977. Studies on the impact of paths on the dune vegetation at Winterton, Norfolk, England. *Biol. Conserv.* 12: 203-206.
- Boyce, S.G. 1954. The salt spray community. *Ecol. Monogr.* 24: 29-67.
- Braun-Blanquet, J. 1932. *Plant Sociology: The study of plant communities.* Fuller and Conard, U.S.A. 439 pp.
- Bray, J.R. and J.T. Curtis. 1957. An ordination of the up-land forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Buckman, H.O. and Brady, N.C. 1960. *The Nature & Properties of Soils.* 6th edit. The Macmillan Co., N.Y. 567 pp.
- Burgess, R.L. 1965. A study of plant succession in the sand-hills of southeastern North Dakota. *Proc. N. Dakota Acad. Sci.* 19: 62-80.
- Chadwick, H.W. and P.D. Dalke. 1965. Plant succession on dune sands in Fremont County, Idaho. *Ecology*, 46: 765-780.
- Chandapillai, M.M. 1970. Variation in fixed dune vegetation at Newborough Warren, Anglesey. *J. Ecol.* 58: 193-201.
- Chappell, H.G., J.F. Ainsworth, R.A.D. Cameron, and M. Redfern. 1971. The effect of trampling on a chalk grass-land ecosystem. *J. Appl. Ecol.* 8: 869-882.
- Cieslinski, T.J. and J.A. Wagar. 1970. Predicting the durability of forest recreation sites in northern Utah--Preliminary results. USDA Forest Service, Research Note INT-117, 7pp.
- Clarke, S.E., J.A. Campbell and J.B. Campbell. 1942. An ecological and grazing capacity study of the native grass pastures in southern Alberta, Saskatchewan and Manitoba. *Tech. Bull. Dept. Agric. Can.* 44.
- Cole, D.N. 1978. Estimating the susceptibility of wildland vegetation to trailside alteration. *J. Appl. Ecol.* 15: 281-286.

- Cordes, L.D., S.L. Hartwell, W.L. Strong. 1975. Environmental assessment of the Pine Lake area, Wood Buffalo National Park. National and Historic Parks Branch, Dept. of Indian Affairs and Northern Development, Canada, 213pp.
- Coupland, R.T. 1950. Ecology of mixed prairie in Canada. Ecol. Monogr. 20: 271-315.
- . 1961. A reconsideration of grassland classification in the northern great plains of North America. J. Ecol. 49: 135-167.
- Coupland, R.T. and R.E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. J. Ecol. 53: 475-507.
- Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz. 27: 95-117, 167-202, 281-308, 361-391.
- Crawford, A.K. and M.J. Liddle. 1977. The effect of trampling on neutral grassland. Biol. Conserv. 12: 135-142.
- Criddle, N. 1927. A calendar of flowers. Can. Field. Nat. 41: 48-55.
- Crum, H. 1976. Mosses of the Great Lakes Forest. University of Michigan Herbarium, Ann Arbor, Mich. 404 pp.
- Curtis, J.T. 1955. A prairie continuum in Wisconsin. Ecol. 36: 558-566.
- Dale, D. and T. Weaver. 1974. Trampling effects on vegetation of the trail corridors of North Rocky Mountain forests. J. Appl. Ecol. 11: 767-772.
- David, P.P. 1971. The Brookdale Road section and its significance in the chronological studies of dune activities in the Brandon sand hills of Manitoba. Geol. Assoc. Canada. Special Paper 9: 293-299.
- Davies, J.F. and B.B. Bannatyne, G.S. Barry, and H.R. McCabe. 1962. Geology and Mineral Resources of Manitoba, Province of Manitoba, Dept. Mines and Natural Resources, Winnipeg.
- Davies, W. 1938. Vegetation of grass verges and other excessively trodden habitats. J. Ecol. 26: 28-49.

- Dowding, E.S. 1929. The vegetation of Alberta. III. The sandhill areas of central Alberta with particular reference to the ecology of Arceuthobium americanum Nutt. J. Ecol. 17: 82-105.
- Dubois, J.E. 1976. The Sandhills of Manitoba, Manitoba Musuem of Man and Nature, Winnipeg, 41 pp.
- Ehrlich, W.A., E.A. Poyser and L.E. Pratt. 1957. Report of Reconnaissance Soil Survey of Carberry Map Sheet Area, Soils Report 7. Manitoba Soil Survey, Manitoba Department of Agric. and Immigration.
- Gates, F.C. 1950. The disappearing Sleeping Bear Dune. Ecology 31: 386-392.
- Gleason, H.A. 1927. Further views on the succession concept. Ecology 8: 299-326.
- Goldsmith, F.B., R.J.C. Munton, and A. Warren. 1970. The impact of recreation on the ecology and amenity of semi-natural areas: methods of investigation used in the Isles of Scilly. Biol. J. Linn. Soc. 2:287-306.
- Hack, J.T. 1941. Dunes of the western Navajo country. Geogr. Rev. 31: 240-263.
- Hale, M.E. 1969. How to Know the Lichens. Wm C. Brown Co. Dubuque, Iowa. 226 pp.
- Hanson, H.C. 1938. Ecology of the grassland. Bot. Rev. 4: 51-82.
- \_\_\_\_\_. 1955. Characteristics of the Stipa comata-Bouteloua gracilis-Bouteloua curtipendula association in northern Colorado. Ecology, 36: 269-280.
- Hanson, H.C. and W. Whitman. 1938. Characteristics of major grassland types in western North Dakota. Ecol. Monogr. 8: 57-114.
- Hepburn, I. 1952. The vegetation of the sand dunes of Camel estuary, North Cornwall. J. Ecol. 32: 180-192.
- Hulett, G.K., R.T. Coupland and R.L. Dix. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. Can. J. Bot. 44: 1307-1331.
- Jamison, V.C. 1956. Pertinent factors governing the availability of soil moisture to plants. Soil Sci. 81: 459-471.

- Kellomaki, S. and V.L. Saastomoinen. 1975. Trampling tolerance of forest vegetation. *Acta Forrestalia Fennica*, 147: 1-27.
- Kilmer, V.J. and L.T. Alexander. 1949. Methods of making mechanical analyses of soils. *Soil Sci.* 68:15-24.
- Kumler, M.L. 1969. Plant succession on the sand dunes of the Oregon coast. *Ecology*, 50: 695-704.
- Lamoureux, G. and M.M. Grandtner. 1977. Contribution à l'étude écologique des dunes mobiles. I. Les éléments phytosociologiques. *Can. J. Bot.* 55: 158-171.
- Landals M. and G.W. Scotter. 1973. Visitor Impact on Meadows near Lake O'Hara, Yoho National Park. Canadian Wildlife Service. 184pp.
- Landsberg, S.Y. 1956. The orientation of dunes in Britain and Denmark in relation to wind. *Geogr. J.* 22: 176-189.
- LaPage, W.F. 1963. A study of vegetative survival and recreation use. Upper Darby, Penn. N.E. Forest Exp. Stat. Progress Report.
- . 1967. Some observations on camp ground trampling and ground cover response. U.S. Forest Service Research Paper, NE-68, 11pp.
- Lauenroth, W.K. and W.C. Whitman. 1977. Dynamics of dry matter production in a mixed-grass prairie in western North Dakota. *Oecologia*, 27, 339-351.
- Leach, W. 1931. On the importance of some mosses as pioneers on unstable soils. *J. Ecol.* 19: 98- 102.
- Liddle, M.J. 1973. The effects of trampling and vehicles on natural vegetation. Ph.D. thesis, University of Wales.
- . 1975. A selective review of the ecological effects of human trampling on natural ecosystems. *Biol. Conserv.*, 7: 17-36.
- Liddle, M.J. and P. Greig-Smith. 1975a. A survey of tracks and paths in a sand dune ecosystem. I. Soils. *J. Appl. Ecol.* 12: 893-908.
- . 1975b. A survey of tracks and paths in a sand dune ecosystem. II. Vegetation. *J. Appl. Ecol.* 12: 909-930.

- Liddle, M.J. and K.G. Moore. 1974. The micorclimate of sand dune tracks: The relative contribution of vegetation removal and soil compression. *J. Appl. Ecol.* 11: 1057-1068.
- McBride, J.R. and E.C. Stone. 1976. Plant succession on the sand dunes of the Monterey Peninsula, California. *Am Mid. Nat.* 96: 118-132.
- Morrison, R.G. and G.A. Yarranton. 1973. Diversity, richness and evenness during a primary sand dune succession at Grand Bend Ontario. *Can. J. Bot.* 51: 2401-2411.
- . 1974. Vegetational heterogeneity during a primary sand dune succession. *Can. J. Bot.* 52: 397-410.
- Moss, E.H. 1944. The prairie and associated vegetation of southwestern Alberta. *Can. J. Res.* 22C: 11-31.
- Mueller-Dombois, D. and H. Ellenberg, 1974. *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York, N.Y. 547 pp.
- Munsell Soil Color Charts. 1954. Munsell Color Company, Inc. Baltimore Maryland.
- Nero, R.W. 1971. The Strange Sandhills of Carberry. Conservation Comment. Manitoba Dept. of Mines, Resources and Environmental Management, Extension Branch, Winnipeg. 8 pp.
- Newsome R.D. and R.L. Dix. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. *Am. Mid. Nat.* 80: 118-185.
- Odynsky, W. 1958. U-shaped dunes and effective wind direction in Alberta. *Can. J. Soil Sci.* 38: 57-62.
- Oliver, R.L.A. 1971. Environmentally controlled experiments in a study of sand-dune colonization by mosses. *Trans. Brit. Bryol. Soc.* 6: 296-305.
- Olmstead, C.E. 1937. Vegetation of certain sand plains of Connecticut. *Bot. Gaz.* 99: 209-300.
- Olson, J.S. 1958a. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.* 119: 125-170.
- . 1958b. Lake Michigan dune development. I. Wind velocity profiles. *J. Geol.* 66: 254-263.
- . 1958c. Lake Michigan dune development. II. Plants as agents and tools in geomorphology. *J. Geol.* 66: 345-351.



- Oosting, H.J. and W.D. Billings. 1942. Factors affecting vegetational zonation on coastal dunes. *Ecology*, 23: 131-142.
- Pool, R.J. 1916. A study of the vegetation of the sandhills of Nebraska. *Minn. Bot. Studies*. 4: 188-312.
- Ramaley, F. 1939. Sand-hill vegetation of northeastern Colorado. *Ecol. Monogr.* 9: 1-51.
- Ranwell, D. 1958. Movement of vegetated sand dunes at Newborough Warren, Anglesey. *J. Ecol.* 46: 83-100.
- 1959. Newborough Warren, Anglesey. I. The dune system and dune slack habitat. *J. Ecol.* 47: 571-601.
- 1960. Newborough Warren, Anglesey. II. Plant associates and successional cycles of the sand dune and dune slack vegetation. *J. Ecol.* 48: 117-141.
- 1972. *Ecology of Salt Marshes and Sand Dunes*, Chapman and Hall, London. 258 pp.
- Richards, P.W. 1929. Notes on the ecology of the bryophytes and lichens at Blakeney Point, Norfolk. *J. Ecol.* 17: 125-140.
- Ritchie, J.C. 1976. The late quaternary vegetation history of the western interior of Canada. *Can. J. Bot.* 54: 1793-1818.
- Rothenberger, S.J., G.E. Larson W.T. Barker, and D.S. Galitz. 1976. Plant growth community analysis in the vicinity of Stanton, North Dakota. *Proc. N. Dakota Acad. Sci.* Abs. 30: 39.
- Rowe, J.S. 1972. *Forest Regions of Canada*. Dept. of Env. Canadian Forestry Service, Publ. 1300. 172pp.
- Salisbury, E.J. 1925. Notes on the edaphic succession in some dune soils with special reference to the time factor. *J. Ecol.* 13: 322-328.
- 1934. On the day temperatures of sand dunes in relation to the vegetation at Blakeney Point, Norfolk. *Trans. Norfolk and Norwich Nat. Soc.* 13: 333-355.
- 1952. *Downs and Dunes*. Bell Publishers, London. 328 pp.
- Sarvis, J.T. 1941. Grazing investigations on the northern Great Plains. *Bull. N. Dakota Agric. Expt. Stn.* 308.

- Scoggan, H.J. 1957. Flora of Manitoba. National Museum of Canada. Bulletin No. 140, Ottawa. 619 pp.
- Shay, J.M. and C.T. Shay. 1979. Vegetation and impact study of Deep Lake, Riding Mountain National Park. Parks Canada, Prairie Region, Dept. of Env. 135pp.
- Smith, H.T.U. 1934. Sand dune cycles in western Kansas. Geol. Soc. Am. Bull. 50: 1934-1935.
- Steiger, T.L. 1930. Structure of prairie vegetation. Ecology, 11: 170-217.
- Swan, J.M.A., and R.L. Dix. 1966. The phytosociological structure of upland forest at Candle Lake, Saskatchewan. J. Ecol. 54: 13-40.
- Thorntwaite, C.W. 1931. The climates of North America according to a new classification. Geogr. Rev. 21: 633-655.
- Tolstead, W. L. 1942. Vegetation of the northern part of Cherry County, Nebraska. Ecol. Monogr. 12: 253-292.
- Van Denack, J.M. 1961. An ecological analysis of the sand dune complex in Point Beach State Forest, Two Rivers, Wisconsin. Bot. Gaz. 122: 155-174
- van der Valk, A.G. 1974a. Environmental factors controlling the distribution of forbs on coastal foredunes in Cape Hatteras National Seashore. Can. J. Bot. 52: 1057-1073.
- . 1974b. Mineral cycling in coastal foredune plant communities in Cape Hatteras National Seashore. Ecology, 55: 1349-1358.
- Wagar, J.A. 1961. How to predict which vegetated areas will stand up best under "active" recreation. Am. J. Recreation, 1: 20-21.
- . 1964. The carrying capacity of wild lands for recreation. Forest Science Monograph 7, 24pp.
- . 1967. Simulated trampling as a technique in recreation research. International Union of Forestry Research Organization, Congress, 14th, Munchen, Paper VII, Section 26, 239-245.
- Waterman, W.G. 1919. Development of root systems under dune conditions. Bot. Gaz. 68: 22-53.

- Watson, W. 1918. Cryptogamic vegetation of the sand dunes of the west coast of England. *J. Ecol.* 6: 126-143.
- Weaver, J.E. and T.J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of tall-grass prairie. *Bot. Gaz.* 93: 113-150.
- \_\_\_\_\_. 1934. The prairie. *Ecol. Monogr.* 4: 109-295.
- Weaver, T. and D. Dale. 1978. Trampling effects of hikers, motorcycles and horses in meadows and forests. *J. Appl. Ecol.* 15: 451-457.
- Wells, B.W. and I.V. Shunk. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: An ecological study. *Ecol. Monogr.* 1: 465-520.
- Willard, B.E. and J.W. Marr. 1970. Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. *Biol. Conserv.* 2: 257-265.
- \_\_\_\_\_. 1971. Recovery of alpine tundra under protection after damage by human activities in the Rocky Mountains of Colorado. *Biol. Conserv.* 3: 181-190.
- Willis, A.J. 1963. Braunton Burrows: The effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* 51: 353-374.
- Willis, A.J., B.F. Folkes, J.F. Hope-Simpson and E.W. Yemm. 1959. Braunton Burrows: The dune system and its vegetation. *J. Ecol.* 47: 1-24, 249-258.
- Willis, A.J. and E.W. Yemm. 1961. Braunton Burrows: Mineral nutrient status of the dune soils. *J. Ecol.* 49: 377-390.
- Wrigley, R.E. 1974. Mammals of the sandhills of southwestern Manitoba. *Can. Field Nat.* 88: 21-39.
- Zimmerman, U.D. and C.L. Kucera. 1977. Effects of composition changes on productivity and biomass relationships in tall grass prairie. *Am. Mid. Nat.* 97: 465-469.

# APPENDIX A

Ranges for soil properties.

Property	Depth cm	Site I bare dune	Site II intermediate	Site III	Site IV prairie
pH	0-5	8.2-8.4	7.7-7.9	7.4-7.9	7.3-7.8
	40-60	7.2-8.4	8.2-8.3	8.0-8.3	7.7-8.2
Organic matter (percent)	0-5	0-0.2	0.7-1.6	0.2-0.4	2.0-5.3
	40-60	0-0.3	0.2-0.5	0.2-0.8	0.3-0.9
Conductivity (micro mho)	0-5	100-120	175-210	160-355	320-800
	40-60	110-130	95-180	105-170	155-250
Nitrogen (nitrate) (ppm)	0-5	0.2-0.6	0.2-2.6	0.8-2.2	2.4-8.2
	40-60	0.2-0.4	0.4-0.4	0.2-1.6	0-3.4
Phosphorus (available) (ppm)	0-5	1.0-1.2	1.4-2.8	1.4-5.2	0.6-2.4
	40-60	1.2-2.8	0.8-1.0	0.8-2.2	0-3.4
Potassium (available) (ppm)	0-5	23-33	25-33	38-85	80-116
	40-60	25-30	20-26	18-32	21-40

Appendix A. continued

Particle size (mm)  
(percent weight)

> 0.5 mm	0-5	3-18	1-5	2-7	3-5
	40-60	0-9	1-9	2-5	0-8
> 0.25	0-5	62-79	54-79	33-55	23-29
	40-60	59-70	57-71	61-85	44-70
> 0.105	0-5	14-29	30-34	34-48	46-60
	40-60	21-38	22-41	10-35	23-50
> 0.053	0-5	0-2	0-2	4-12	11-19
	40-60	1-2	1	0-5	0-2
< 0.053	0-5	0	0	0-2	3-7
	40-60	0	0	0	0