Geomorphic Processes and Vegetational Change along the Meade River Sand Bluffs in Northern Alaska

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ABSTRACT. Geomorphic processes within the region of sand deposits on the Alaskan Arctic coastal plain bring about changes in local environments, and consequently in local vegetation, through time. Geomorphic processes and vegetational patterns on bluffs are related to the directions which the bluffs face with respect to prevailing winds. Caribou and ground squirrels augment wind erosion of the bluffs by disturbing the vegetation while grazing, trampling or burrowing. Environmentally induced vegetational changes resulting from continued geomorphic and animal disturbances are more common than autogenic successions which, being generally accompanied by rising permafrost, help to stabilize sands. Vegetational sequences existing along the bluffs result from the interaction of both linear and cyclic changes in the ecosystem.

RÉSUMÉ. *Les processus géomorphologiques et les changements présentés par la végétation le long des falaises de sable du fleuve Meade en Alaska du nord.* Les processus géomorphologiques dans les régions de gisements de sables le long de la plaine cotière de l'Alaska arctique entraînent, avec le passage du temps, des modifications locales et, par conséquent, de la végétation locale. Les processus géomorphologiques et la distribution de la végétation des falaises sont en relation avec l'orientation de celles-ci par rapport aux vents dominants. Les caribous et les tamias ajoutent à l'érosion des vents en altérant la végétation lorsqu'ils broutent, piétinent ou creusent. Les modifications de la végétation dues à l'environnement et qui sont le résultat de perturbations continues géomorphologiques et animales, sont plus fréquentes que les successions autogènes qui, étant généralement accompagnées d'une élévation du niveau du pergélisol, contribuent à la stabilisation du sable. La manière dont la végétation évolue le long des falaises est le résultat des changements tant linéaires que cycliques dans le système écologique.

РЕЗЮМЕ. *Геоморфные процессы и изменения в растительности на отвесных песчаных берегах р. Мид в северной части Аляски.* Геоморфные процессы в районе песчаных отложений на омываемом Северным Ледовитым океаном Аляскинском плато ведут с течением времени к изменениям в местной окружающей среде, а, следовательно, и в местной растительности. Геоморфные процессы и распределение растительности на песчаных обрывах зависят от того, куда обращены берега по отношению к ветрам преобладающего направления. Выпас карибу и норы сусликов усиливают ветровую эрозию обрывов. Связанные с нарушениями в геоморфных процессах и со сдвигами в животном мире изменения растительности более типичны, чем автогенная сукцессия, которая, сопровождаясь обычно повышением уровня многолетней мерзлоты, содействует стабилизации песков. Сочетание растительности, наблюдаемое вдоль отвесных берегов, является результатом взаимодействия линейных и циклических изменений в экосистеме.

INTRODUCTION

Sand deposits, because of their susceptibility to erosion by wind, provide ideal sites for research on vegetational change through time. Ecologists have used dunes

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to study the principles of vegetational succession since publication of the pioneer papers of Warming (1891) and Cowles (1899). Similar patterns and processes occur on a variety of inland and coastal dunes.

The focus of our research has been to describe vegetational changes on tundra sands in relation to geomorphic processes operating in an Arctic milieu. The erosion and deposition of sand by wind in the tundra, although modified by permafrost, produces patterns of colonization and stabilization similar to those produced in temperate regions. In contrast, ice-wedge polygons and thermokarst erosion produce patterns which have no counterpart in temperate region sand deposits. Thaw depths in the area range from a few centimetres to over one metre.

Our research sites are located along portions of the Meade River approximately 100 km south of Barrow, Alaska, near the new native village of Atkasook (Fig. 1). In the central Meade River area, an extensive clean, well-sorted sand deposit of marine origin mantles underlying sediments and rock. These sands vary in thickness from about five to ten metres in our research area. They represent the Meade River unit of the Gubik Formation which was unconformably deposited in a shallow near-shore shelf environment over cretaceous rocks (Black 1964). In places, these rocks now form the riverbed. The sands have been reworked considerably by wind and water. The region is characterized by only slight (a few metres) topographic relief. However, the river has cut through the Gubik sediments producing bluffs and cutbanks (Fig. 2) as much as 10 m in height. Oriented lakes are numerous, and many of them are currently expanding and producing small bluffs. Other lakes have in the past produced small bluffs, which today mark the margins of drained, or partially drained, lake basins. The erosion of such lake and river bluffs and cutbanks results in the characteristic local vegetational patterns. These spatial patterns are indicative of vegetational changes which take place through time as bluff erosion continues.

In addition to numerous oriented lakes, common surficial features include areas of low-centre ice-wedge polygons and stabilized aeolian sand deposits. These deposits appear to be relatively flat or gently sloping; their vegetation is dominated

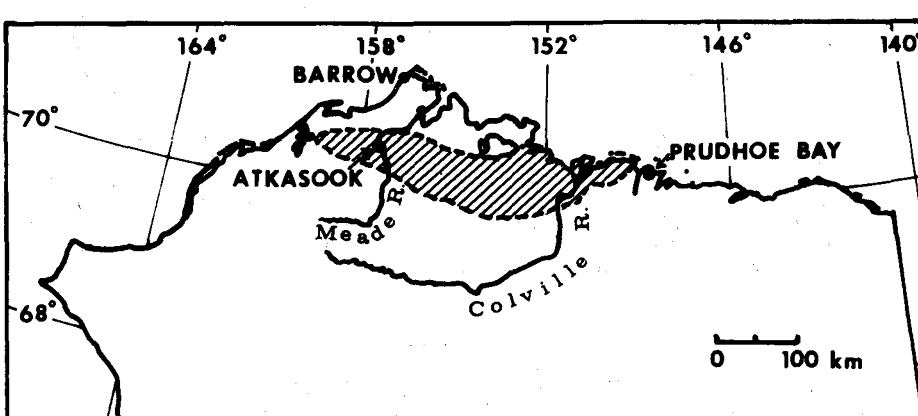


FIG. 1. Map showing the location of the research sites. Sand dunes are common within the area indicated by shading.

FIG. 2. View of a river bluff. At this site, moderate deposition of sand by wind obscures polygon form at the bluff edge.

by the tussock-forming sedge *Eriophorum vaginatum*. Black (1951) describes these oldest and most common deposits as stabilized dunes. He states the hypothesis that deeper thaws, reduced surface moisture, and diminished vegetational cover which probably accompanied a period of higher temperatures in post-Pleistocene times may have been responsible for such dune formation. Aeolian erosion and deposition of sand, although not as extensive as in the past, is still occurring, particularly along bluffs and cutbanks.

Vegetational changes on the bluffs result both from disturbances and from autogenic vegetational successions. Most disturbances are due to geomorphic processes; however, disturbances by animals also are important. Up to now, there has been little disturbance by man. Most vegetational changes which occur along these bluffs result directly or indirectly from one of the following:

1. Environmental changes associated with bluff formation and continuing river or lake erosion.
2. Thermokarst erosion.
3. Wind erosion and deposition of sand (often augmented by disturbance due to animals).
4. Autogenic vegetational succession (associated with soil development).

METHODS

Aerial photographs and maps of the research area were used both in the interpretation of topographic features and in the location of study plots and transects. Bluffs formed by past river erosion may be delineated easily on photographs and distinguished from those caused by past lake erosion. The relative ages of most

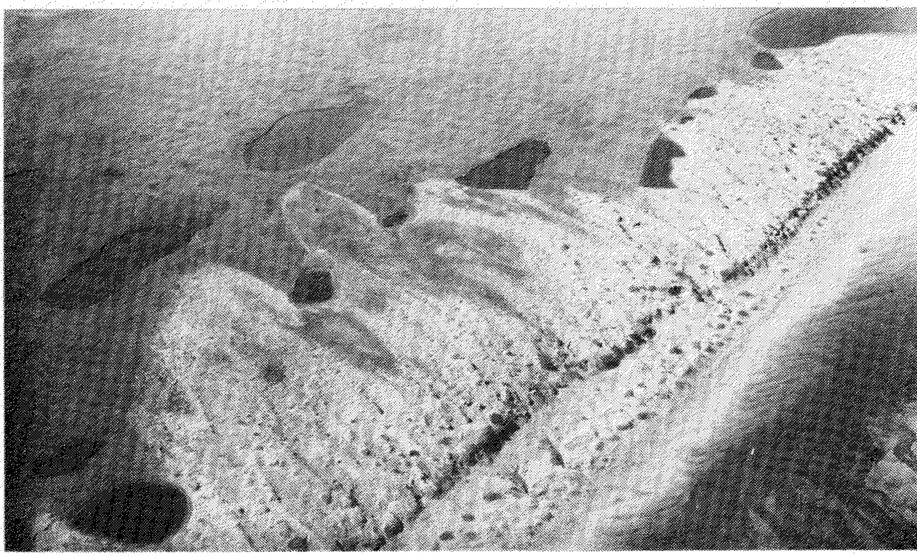


FIG. 3. Oblique aerial view of sand dunes and "sand tongues" on a small river bluff. The river is low, exposing river-bar sands which are blown into the *Salix* dunes and eventually onto the adjacent tundra. These sands cover polygons and even shallow lakes. The "sand tongue" which reaches farthest from the river (left-centre) is semi-stabilized with vegetation.

geomorphic features, especially parabolic dunes, can also be determined by indications of overlapping as seen from the air. Many flattened, often stabilized, depositional forms ("sand tongues") which might be overlooked from the ground are obvious from the air (Fig. 3).

A variety of bluff forms and associated features were selected, and transects five metres wide, and between 50 m and 247 m long, were marked out perpendicular to these forms. At one site, where patterned ground occupies the area next to a bluff face, a five-metre-wide transect was insufficient to describe the results of interacting erosion of bluffs and activity of ice-wedge polygons. At this site, a grid (40 m x 140 m) was marked out. A survey of bluffs was conducted by boat and on foot to be certain that the sites selected were representative of the area. A total of 20 transects were established and permanently marked with steel stakes. The data presented below come from representative sites.

The vegetation was sampled at five-metre intervals along the transects using a 50 cm x 20 cm quadrat frame. The percentage areal coverage by each species and by dead material was recorded. In addition, a map of vegetation types was made for each transect; the dominant species as well as other species present were recorded. Voucher specimens of plants were collected and placed in the Duke University Herbarium. The nomenclature used for vascular plant species follows Hultén (1968).

Vertical profiles of several of the transects were drawn using a clinometer. Depth of thaw was determined using a calibrated metal probe, and was measured at one-metre intervals along transects. Soil moisture was measured gravimetrically throughout the season from samples collected at representative sites on or near transects. Soil samples were collected from topographically or vegetationally distinct areas for analysis of total and available nitrogen, phosphorus, potassium, calcium, magnesium, and pH and loss-on-ignition. Soil samples from a single river-bluff transect were subjected to laboratory analysis to determine particle size distribution and quantity of organic matter.

RESULTS

Degree of wind erosion of bluffs is determined primarily by bluff aspect. Winds are so strongly bimodal in direction (being principally east-northeast and west-southwest) that they control orientation of dunes, lakes and sand blowouts (Livingstone 1954; Carson and Hussey 1959). The geomorphic processes and vegetational changes associated with bluffs may be more easily understood if one considers the following categories:

1. Bluffs which face away from the principal wind directions and therefore show little or no wind erosion and deposition of sands.
2. Bluffs which face neither toward nor away from the prevailing winds, and which show a range of wind erosion and deposition effects.
3. Bluffs which face the prevailing winds and therefore show extreme effects of wind erosion and deposition of sands.

Bluffs exhibiting minimum effects of wind:

Bluffs of this type generally show the familiar but truncated patterns of ice-wedge polygons. Transition in polygon form usually exists from the bluff top into the adjacent tundra. These transitions in polygon form result from the conversion of low-centre polygons to high-centre polygons. Such a conversion is induced by lateral drainage at a steep bluff edge. Lateral drainage of ice-wedge troughs intersected by a bluff face promotes the formation of thermokarst gullies. As ice-wedges, which underlie the troughs, are exposed at the bluff edge, they begin to melt; this results in thermokarst in the troughs. The meltwater drains toward the river along the trough-bottoms over the tops of ice-wedges, increasing the melting of ground ice. As the ice-wedges which surround polygons melt, polygon troughs and rims slump; in the process, the old polygon basins are left high and dry. This change from low-centre polygons to high-centre polygons may require several decades or more, depending upon the rate of bluff erosion by the river. Secondary and tertiary ice-wedges often show little or no surficial expression in large low-centre polygons. As a consequence, more than one high-centre polygon can result from the thermokarst erosion of a single low-centre polygon. (The general increase in the density of polygons toward the bluff edge may be noted in Fig. 4.)

The centres and troughs of low-centre polygons often contain standing water well into the growing season. Water depth of polygon centres varies seasonally, but is usually in the range of 20-30 cm. As polygon rims slump, their impounding effect disappears and with it any standing water in the centres of transitional and high-centre polygons.

The vegetational changes associated with the development of high-centre polygons along bluffs have been inferred from spatial analogy (see Fig. 4). Almost

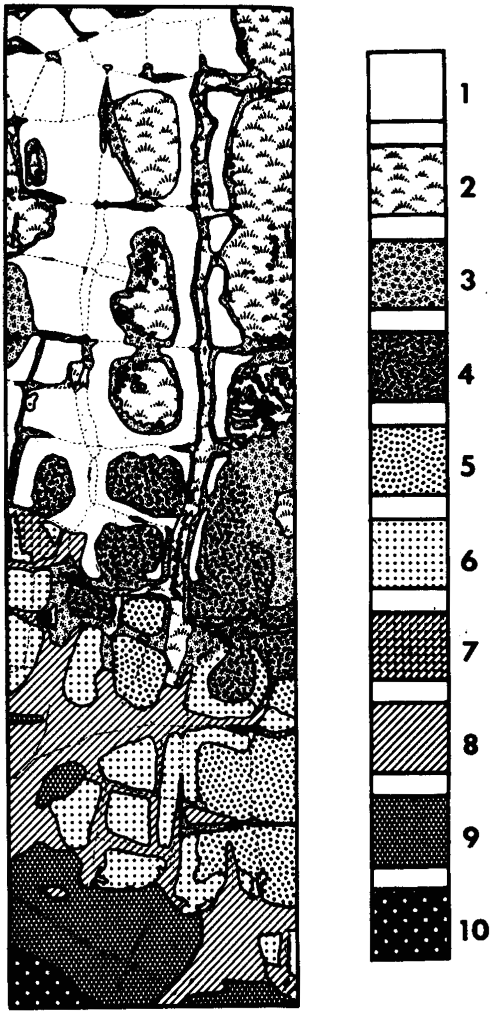


FIG. 4. Grid 40 m x 140 m showing the vegetation associated with low-centre, transitional and high-centre polygons at a bluff edge: 1. polygon rims with *Eriophorum vaginatum, Ledum palustre, Alectoria* spp., *Vaccinium vitis-idaea, Cassiope tetragona* and *Diapensia lapponica;* 2. *Carex aquatilis* seasonal ponds; 3. Mosses (primarily *Sphagnum*), *Rubus chamaemorus, Carex aquatilis* and *Betula nana;* 4. *Carex aquatilis; Aulacomnium* spp., *Bartramia pomiformis, Salix pulchra* and some *Sphagnum;* 5. *Carex bigelowii, Aulacomnium* spp., *Dicranum* spp., *Bartramia pomiformis, Salix pulchra, S. reticulata,* very little *Carex aquatilis* and no *Sphagnum;* 6. *Dryas integrifolia, Polygonum bistorta, Diapensia lapponica, Thamnolia* spp., *Cetraria cucullata, Salix pulchra, Salix reticulata* and *Silene acaulis;* 7. Similar to type 1, but lacking *Eriophorum* and with mosses and lichens dominating; 8. eroded troughs with *Boykinia richardsonii, Cassiope tetragona, Salix lanata, Aulacomnium* and other mosses, *Pyrola grandiflora, Salix pulchra, Salix reticulata* and *Betula nana;* 9. bare sand on the steep bluff face; 10. river. The dashed lines indicate ice-wedge locations determined by soil cracks or other evidence.

pure stands of *Carex aquatilis* constitute the vegetation of the centres and troughs of ponded low-centre polygons. On these polygon rims, there is a mixture of upland tundra species including *Eriophorum vaginatum, Ledum palustre, Rubus chamaemorus, Vaccinium vitis-idaea, Bartramia pomiformis* Hedw., *Alectoria* spp., and *Cetraria cucullata* (Bell.) Ach. The species on rims of low-centre polygons largely disappear as the rims disappear. The result is the formation of high-centre polygons covered with a different vegetational type on the tops of the bluffs. In contrast, high-centre polygons in some less exposed sites maintain those species characteristic of the rims of low-centre polygons.

As the polygon centres drain, *Sphagnum* colonizes the bare peat between the stems of *Carex aquatilis*, moving in from the polygon sides and from "islands" of moss in the low-centre polygon basins.

The mosses *Bartramia pomiformis* and *Aulacomnium* spp. invade as drainage continues. *Salix pulchra* also becomes conspicuous as moss coverage increases.

With continued drainage, *Sphagnum* disappears, and *Salix reticulata* becomes important. *Carex bigelowii* invades and eventually replaces *Carex aquatilis* when sites have become well-drained. *Carex bigelowii* decreases in coverage as high-centre polygons become exposed to the conditions at the bluff edge, where *Dryas integrifolia, Polygonum bistorta, Diapensia lapponica, Thamnolia vermicularis* (Sw.) Ach., *Silene acaulis* and *Cetraria cucullata* invade. *Dryas* dominates the polygon centres at the end of this sequence near the bluff edge.

In the troughs, *Carex aquatilis* gives way to a mixture of species including *Boykinia richardsonii, Cassiope tetragona, Pyrola grandiflora, Salix pulchra, Salix reticulata, Salix lanata, Betula nana, Aulacomnium* spp. and other mosses. This vegetational type is heterogeneous and often is associated with bare soil where slumping has caused vegetation to be displaced.

Although changes in soil moisture accompany high-centre polygon formation on bluffs, other changes are occurring as well. As drainage proceeds, soil aeration increases, allowing an increased rate of organic-matter decomposition. The high organic-matter content of the wet peaty soils in polygon centres decreases through low-centre, transitional, and high-centre polygon soils (see Table 1). A related result is a trend to higher pH and changes in the proportions of available nutrients. Not all changes in nutrient status can be related to changes in soil organic matter. In non-saturated soils in this area, availability of phosphorus and potassium generally decreases with increased organic-matter content, while availability of ammo-

TABLE 1. Soil nutrients, pH and organic matter at depths of 0-30 cm at three bluff sites.

SITE	POSITION	pH	LOSS-ON-IGNITION (%)	AVAILABLE NUTRIENTS (parts per million) Ammonium	Nitrate	Phosphorus	Potassium	Calcium	Magnesium
Polygon transect on bluff (Little effect of wind)	High-centre polygons	5.63	11.90	26.0	7.8	4.6	55.6	1,192.5	222.1
	Transitional polygons	5.16	23.46	39.8	9.7	2.2	48.6	787.5	154.5
	Low-centre polygons	4.94	25.85	35.5	5.2	3.0	51.3	540.5	102.6
Intermediate bluff transect (Moderate sand deposition)	0-5 m from edge	7.71	1.76	9.3	4.4	8.0	35.8	844.1	53.0
	30-40 m from edge	5.97	5.41	15.8	4.4	6.8	15.5	887.5	111.6
	55-65 m from edge	5.65	14.44	21.0	6.7	5.8	18.2	1,249.0	199.0
Old wind-eroded bluff	*Elymus* and bare sand	5.69	0.79	14.5	6.4	22.1	20.2	149.5	20.4
	Elymus and closed vegetation	5.17	2.90	11.3	5.3	17.3	11.3	165.0	35.3
	Ground squirrel mound	5.18	2.70	47.9	14.1	39.0	82.1	285.0	70.3

nium, nitrate, calcium and magnesium increases with increased organic-matter content. Nutrient availability in saturated soils is, however, not what would be predicted from organic matter alone; retarded decomposition slows release of many nutrients, but availability of phosphorus and potassium is slightly higher in the saturated soil of the low-centre polygon basin than in the soil of the transitional polygon. These nutrients may be limiting to microbial growth; therefore decreased microbial demand for untrients in saturated soils may explain the increase in availability of the nutrients.

As invasion by mosses occurs in this vegetational sequence, the maximum depth of thaw decreases. With continued drainage, and decreased soil moisture (and moss cover), thaw depth again increases. Depth of thaw in trough bottoms changes little, but trough depth increases throughout the polygon-conversion sequence because of gradual loss of ground ice from the tops of the ice-wedges.

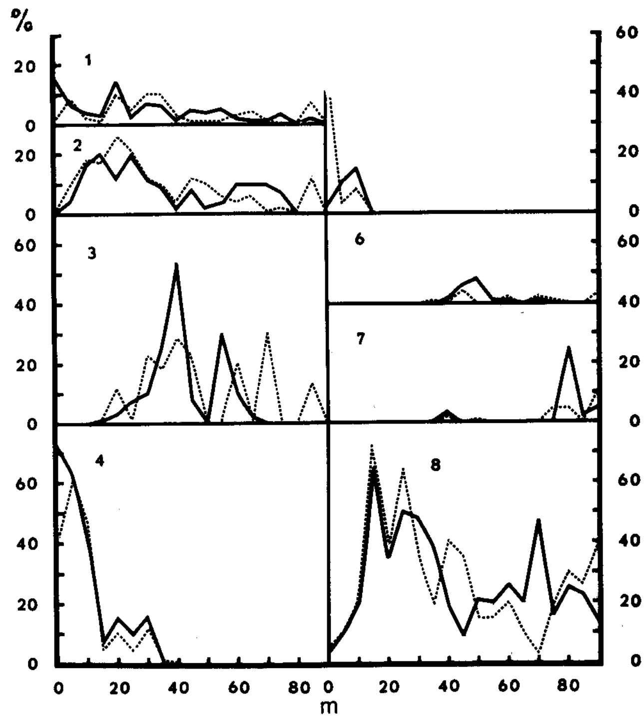
Bluffs moderately affected by wind:

At bluff sites with aspects which allow the deposition of intermediate amounts of sand by wind, surface polygonal patterns are absent or masked. The soil surface is nearly level back from such a bluff edge. Ice-wedges exist on and back from the edges of such bluffs, but sand movement masks their surficial expression. This lack of microtopography allows gradients in several factors to form environmental continua from the bluff edge into the surrounding tundra. This promotes the establishment of a vegetational continuum at such sites.

Although the community of plants at the edge of such a bluff differs greatly from that only a few tens of metres away, species vary so much in abundance at these sites that delimitation of vegetation types is difficult. Bare sand generally covers all steep faces of bluffs where erosion is active. Certain species are, however, found on them; they include *Oxyria digyna, Boykinia richardsonii, Salix lanata* and clumps of vegetation (mostly *Dryas integrifolia*) which have fallen from the eroding bluff edge. On top of the bluff edge, bare sand constitutes a larger portion of the aereal coverage relative to vegetation, even at sites where there is only moderate sand deposition. Vegetational coverage increases to 100 per cent within 40 m along one transect running back from such a bluff edge. The absolute distance from the bluff edge at which vegetational distinctions can be made varies among sites, but the order of changes remains consistent.

The percentage cover by selected species at various distances from the bluff edge along the above-mentioned transect is presented in Fig. 5. The edge of the bluff is dominated by *Dryas integrifolia* and scattered individuals of *Salix glauca* (see Fig. 2). *Arctagrostis latifolia* is occasionally found along the edges of similar bluffs; however, this species is absent along the transect. *Dryas* often forms nearly pure mats for a distance behind a bluff edge. *Carex bigelowii* becomes increasingly abundant in the *Dryas* zone farther from the bluff edge and becomes dominant even farther into the adjacent tundra. Mosses are an important component of the vegetation in the *C. bigelowii* zone, and three moss species alternately dominate in the moss-*Carex* zone beyond. *Tomenthypnum nitens* (Hedw.) Loeske is more commonly the dominant species nearer the bluff edge, while *Aulacomnium palustre* (Hedw.) Schwaegr. and *Pleurozium schreberi* (Brid.) Mitt. often dominate the

FIG. 5. Percentage cover of selected cover categories away from a steep bluff edge. Solid lines are data from the northernmost side of the 5-m-wide transect, and broken lines are from the southernmost side. 1. *Dryas integrifolia,* 2. *Carex bigelowii,* 3. *Tomenthypnum nitens,* 4. bare sand, 5. *Salix glauca,* 6. *Eriophorum vaginatum,* 7. *Carex aquatilis,* 8. dead material and litter.



areas further from the bluff. *Carex bigelowii* is conspicuous in this zone, while *Salix pulchra, S. reticulata, Pyrola grandiflora, Cassiope tetragona* and *Eriophorum vaginatum* are locally important.

Vegetational gradients such as the one described above extend into undisturbed areas of low-centre polygons, or old deposits stabilized by upland tundra species. Such vegetational gradients are representative of successions which occur in a community as the bluff edge of a river comes gradually closer to it through erosion — the orientation of the bluff being such that moderate sand deposition occurs.

The gradients in soil moisture and depth of thaw from the edge of such a bluff into the adjacent tundra are shown in Fig. 6. Seasonal and annual variations occur. Maximum depth of thaw (August values) were greater in 1976 than in 1975 over much of this transect. Air temperatures were generally higher during the summer of 1976 than during that of 1975. Near the bluff edge, maximum depth of thaw was deeper in 1975 than in 1976. The reason for this is not clear, but a possible explanation is reduced lateral heat flow by soil water in 1976.

The presence of permafrost prevents deep drainage of soil water, but bluff topography allows lateral drainage from nearby soils. Soil moisture is inversely related to thaw depth at most sites. This fact may be attributed to the large heat capacity of water and to the latent heat associated with melting as a thaw front advances. The relatively large effect of the latent-heat factor on depth of thaw has been demonstrated in a model by Nakano and Brown (1972), which they validated for tundra soils at Barrow, Alaska. An exception to the normal relation-

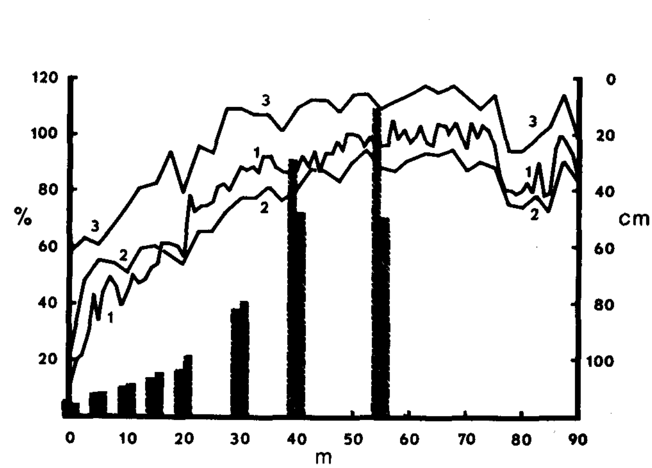


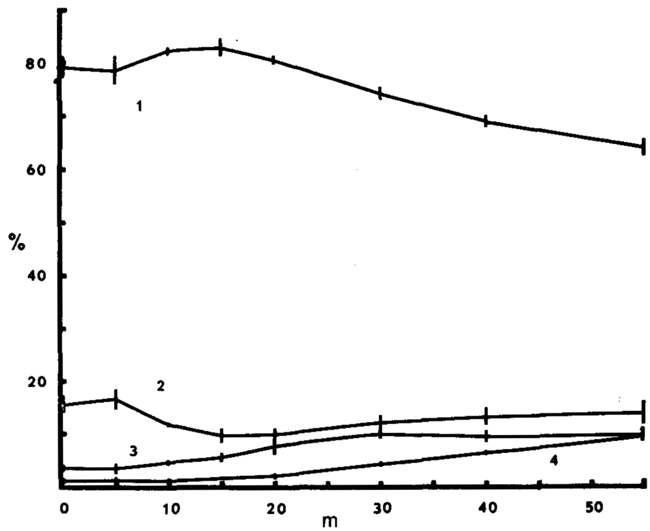
FIG. 6. Depth of thaw (lines) and percentage soil moisture (bars) away from a steep bluff edge. Dates for the depth-of-thaw measurements are: 1. 4 August 1975, 2. 18 August 1976, 3. 29 June 1976. Soil-moisture determinations are from 2 August 1975. The first bar in each pair represents the 0-10 cm depth, and the second bar represents the 10-20 cm depth. Each soil-moisture percentage indicated is the average of three determinations.

ship of soil moisture to depth of thaw exists wherever seasonal ponds develop (note the increased thaw depth under the seasonal ponds near the end of the transect represented in Fig. 6). Here, underlying soils thaw to an intermediate depth even though saturated. Lateral transport of heat by water may play a role in creating deeper thaws in some sites. Also, high transmissivity of shallow water in seasonal ponds and high absorptivity of the black, peaty bottoms probably play important roles. Although loss of heat through evaporation from ponds must occur, it is probably not as great as the loss from nearby moist, moss-covered areas where surfaces allowing evapotranspiration are considerably greater than those of ponds.

The inverse relationship between soil moisture and depth of thaw which exists in many sites is characterized by a positive feedback cycle; a change which reduces soil moisture, such as increased lateral drainage, allows thaw depth to increase so that a greater soil volume is available for the distribution of soil moisture. An increase in soil moisture reduces the depth of a subsequent thaw, and in consequence a reduced soil volume is provided for the distribution of meltwater. The limits of thaw depth are, however, determined by the extent to which dry and saturated soils thaw.

The soils consist primarily of fine sand. Particle segregation by wind and accumulation of organic matter are important factors determining soil variability (Fig. 7). Similar results are reported by Rickert and Tedrow (1967). Soil moisture and its counterpart, soil aeration, largely determine the rate of decomposition or accumulation of organic matter. Organic matter influences pH and nutrient levels and augments the effect of increased moisture upon decreased thaw depth. In moist sites, organic matter is accumulating and permafrost is rising, trapping a portion of the available nutrient pool. Although nutrient analyses are available for only three portions of the transect (Table 1), these suggest that gradients in nutrients exist. These gradients are related to the amount of soil organic matter, as was suggested earlier. Here, however, the lack of saturated soils makes the relationship more clear. The amount of calcium is exceptionally high on this transect relative to the amount of organic matter and suggests past enrichment,

FIG. 7. Soil-particle size distribution and soil organic matter away from a steep bluff edge. 1. fine sand, 2. very fine sand, silt and clay, 3. medium sand, 4. organic matter. Coarse sand was less than one per cent of the total in all samples, and no particles larger than 2 mm in diameter were found. Vertical bars represent the standard error. Organic-matter data in this figure were determined using wet combustion, and compare well with the loss-on-ignition data in Table 1.



possibly by a caribou carcass. Animal carcasses and the antlers of caribou (in the case of calcium) probably play an important role in creating locally high nutrient concentrations.

As would be predicted from the gradation in organic-matter content, the soil is more acidic farther from the bluff edge. The relatively low amount of organic matter on this transect compared to the polygon transect results from greater sand deposition by wind. Sand deposition tends to "dilute" some of the nutrient concentrations in this site compared to the polygon transect as well.

Winter winds blow nearly all bluff edges free of snow. On 20 May 1976, snow accumulations of 0.5 cm, 9.5 cm, and 24.0 cm were measured at 5 m, 35 m and 65 m respectively, from the bluff edge along the transect.

Bluffs greatly affected by wind:

Bluffs which face prevailing winds generally lack the environmental and vegetational continua characteristic of bluffs with moderate sand deposition. This lack of continuity in gradations of environmental factors results from the patchy microtopography associated with wind erosion and deposition of sands on these bluffs. Windward-facing bluffs from which river courses or lake margins have receded are rounded in form and generally have a number of small but active elliptical blowouts. Even the steep bluffs which are currently being eroded by the river have a wind-carved appearance where facing the wind. In addition to having large blowouts, these young bluffs are often capped with "climbing" dunes. Dunes are most common wherever bluffs occur leeward of an exposed riverbar. Sand carried from the bar by wind is dropped on the bluff face and bluff edge. Similar patterns occur on the Colville River delta (Walker 1967).

Where the contours of steep bluffs are interrupted by occasional blowouts and climbing dunes, *Elymus arenarius* subsp. *mollis* invades the open sand, though it seldom provides more than ten per cent coverage. Vegetational gradients, similar to the one described above for the bluff-edge transect, usually surround blowouts and dunes. Eventually, wind blows the higher climbing dunes into large, flattened, parabolic forms. *Dryas integrifolia* and *Arctostaphylos rubra* surround the outer margin of parabolic dunes, and brilliant red arcs may be seen from the air in August as the leaves of *Arctostaphylos* attain autumn coloration. These dunes often impede drainage of the adjacent tundra, thus causing very wet and very dry habitats to abut each other. Parabolic dunes are eventually blown out into flat tongue-shaped deposits ("sand tongues") which may support upland tundra vegetation (see Fig. 3). The vegetational changes which culminate in upland tundra vegetation on sand deposits occur only where relief and soil drainage are slight. Accumulation of organic matter and decreased depth of thaw appear to be important factors in such succession.

In well-drained sites, autogenic succession culminates in a lichen-heath vegetational type dominated by *Alectoria* spp. and characterized by low evergreen shrubs such as *Diapensia lapponica, Vaccinium vitis-idaea* and *Ledum palustre.* The dominance of *Alectoria* spp. (particularly *A. nigricans* (Ach.) Nyl.) over other lichens may result in part from the influence of caribou grazing. Soil development and competition for nutrients are probably important factors in this succession. Autogenic successions on bluffs are generally interrupted by disturbance caused by animals and/or wind erosion and deposition of sands.

On cutbanks and river bars within the valley, willows occur with *Elymus arenarius* in large blowouts, on dune slacks, and on parabolic dunes (see Fig. 3). Four species of willows, *Salix alaxensis, S. lanata, S. glauca* and *S. niphoclada,* are found in active sands. *Salix alaxensis,* however, is usually restricted to river bars and flood-plain margins. A zonational series (of *S. alaxensis,* nearest the river, to *S. lanata* and eventually to *S. glauca,* farthest from the river) occurs on both sand bars and dunes. *Salix niphoclada* is commonly interspersed with these species in active dunes near the river. Fields of small dunes form around willows on old river bars and flood-plains. Of these species, only *Salix glauca* is commonly found away from the river. These local dune areas provide highly specialized niches for certain plant species such as *Mertensia drummondii, Polemonium boreale, Artemisia glomerata,* and *Brayia pilosa* which are at or near their northern limits here. Although these small dunes on river bars and cutbanks are similar to and even intergrade with bluff dunes, attention is concentrated here only on the bluff dunes.

Stabilization of eroding bluffs which face prevailing winds occurs only after the relief has been reduced by winds to a gentle slope and/or adjacent source-areas of sand (i.e., river bars) have themselves become stabilized. Vegetation may become established in areas with pronounced relief only where protected from the winds by aspect or late-lying snowbanks. Windblown snow accumulates along the bluff base and the resulting snowbank, which remains there well into July, provides protection from the wind and ensures increased soil moisture. Thus, a snowbank community exists at the windward base of many eroded bluffs. The open character of the vegetation on the upper, gently sloping portion of an eroded bluff contrasts sharply with the closed vegetation and moist nature of the steep basal, snowbank-protected portion. The snowbank vegetation exhibits some zonation. *Arctagrostis latifolia* and *Polygonum bistorta* are the first to be exposed as a snowbank melts. *Cassiope tetragona, Saxifraga punctata, Petasites frigidus, Oxy-*

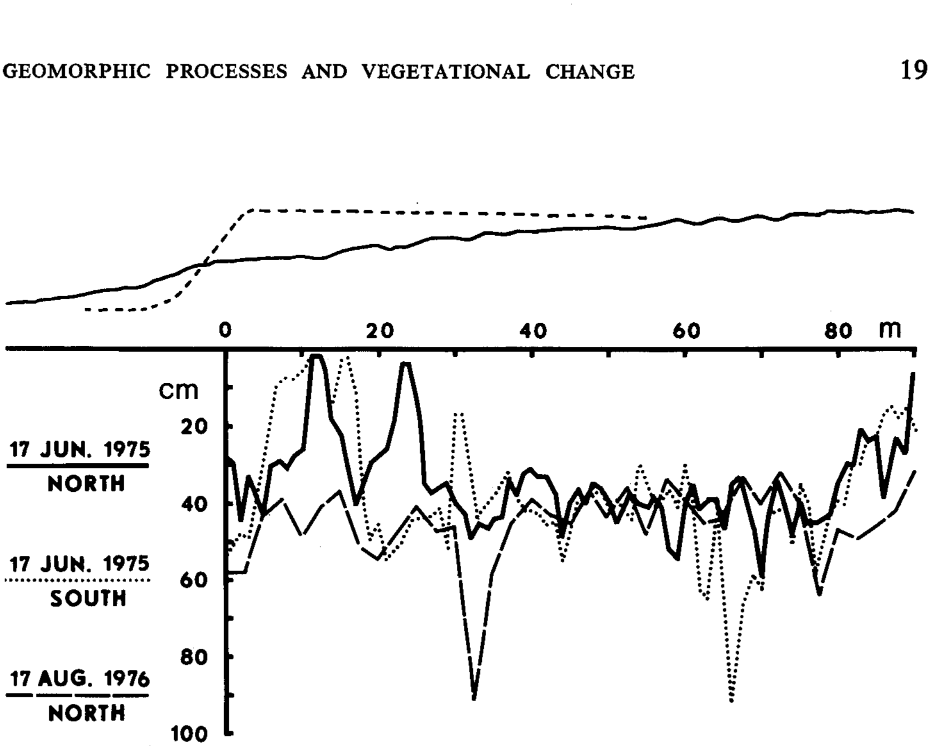


FIG. 8. Bisect of transect (upper solid line) with vertical scale equal to horizontal scale. The broken line indicates hypothetical original bluff form. Depths of thaw along the northernmost and southernmost sides of the upper portion of this transect are plotted below. Note the great variability in thaw depth along the transect and between the sides which are 5 m apart.

ria digyna, Ranunculus nivalis and *Cetraria cucullata* soon appear also. *Salix rotundifolia*, mosses, liverworts, *Carex aquatilis* and *Dupontia fischeri* occur beneath the latest-lying snowbanks.

Vegetation may become temporarily established in some eroding areas, but blowouts often recur until the relief is diminished. Soil moisture as well as depth of thaw on such bluffs is controlled more by the microtopography of blowouts than the mesotopography of bluff form (see Fig. 8). Some eroded bluffs are nearly completely covered with vegetation, primarily *Dryas integrifolia*, and are almost stable. *Salix phlebophylla* and *Betula nana* are important constituents of the vegetation between the upper margin of old eroded bluffs and undisturbed tundra. *Dryas integrifolia* is to be found on the more active bluff dunes only at their depositional margin, but this species is important throughout less active dunes. *Dryas* forms mats in which blowouts can occur.

Grazing and trampling by caribou (*Rangifer tarandus*) and grazing and burrowing by ground squirrels (*Spermophilus parryi*) appear to be of primary importance in the creation of blowouts in partly vegetated sands. The palatability of *Dryas* is probably less significant in attracting animals to these sites than is the relatively snow-free winter condition and the deep thaws of summer. Ground-squirrel burrows are restricted to deep-thawing sites such as bluffs. Evidence also exists for the presence of caribou on bluff areas in winter and early spring. Disturbance to the vegetation by animals causes coverage by vegetation to be reduced, which in turn allows wind erosion to occur.

Ground-squirrel burrows on old eroded bluffs often occur on mounds. These mounds are nutrient-enriched relative to the nearby open sands (Table 1). It seems probable that these mounds form as surrounding soils are eroded by winds. The nutrient enrichment (particularly nitrification) near burrows allows production of greater plant cover and differential erosion rates between mounds and heavily grazed nearby vegetation. Where dunes occur, they may be stabilized by this same mechanism. Price (1971) reported the existence of interactions between ground squirrels and solifluction lobes in an alpine environment, which did not, however, lead to the production of mounds.

The lack of snow cover, which invites disturbance by animals, may also be responsible, in part, for maintaining such barren environments by preventing invasion of certain plant species. Although characteristic of snow-free areas, *Dryas integrifolia* is generally absent wherever wind erosion is active. This species has greater ~~coverage in~~ places where there are moderate rates of sand deposition. *Elymus arenarius* is present in both erosional and depositional areas; it is characterictic of the most active areas. Although *Elymus arenarius* is by far the most notable pioneer of open sands, other species occur in open sites as well. *Carex obtusata*, *Stereocaulon* sp., *Silene acaulis* and *Artemisia borealis* are widely scattered, but are found even in actively eroding sites. Stabilization by *Dryas* mats is often temporary, due to their susceptibility to sand blowouts.

Succession in blowouts on old wind-modified bluffs:

The small elliptical blowouts in wind-rounded bluffs are oriented with their long axes aligned with the prevailing winds. Once formed, these elliptical blowouts create microtopography which causes an alteration in local drainage and in the accumulation of windblown snow. Snow cover plays an important role in slowing erosion and allowing invasion by plants in these blowouts. Vegetational successions, similar to those on dunes and sand tongues, occur at these sites and appear to be in part autogenic. The following vegetational sequence is presented as a typical example:

> Stage 1. Pioneer species vary between the elliptical blowouts. In areas with many blowouts close together, *Elymus arenarius* is the most important invader. *Elymus* is often not present in small isolated blowouts; in such cases, a *Polytrichum* sp. is commonly found as a first invader. An invader which may be common in either case, and which plays an important role, is *Carex obtusata*. Several other species such as *Artemisia borealis* are found sporadically as invaders and play a relatively minor but characteristic role.
>
> Stage 2. Dead leaves of *Elymus* accumulate at the base of the stem and radiate out from it, providing increased cover along the soil surface. *Carex obtusata* grows by rhizomes in long straight rows which catch windblown material, particularly fragments of *Alectoria nigricans*. Both processes may occur sympatrically.
>
> Stage 3. Lichens (including a *Stereocaulon* sp.) begin to provide a large percentage of the cover. Small forbs (particularly *Campanula lasiocarpa*) appear.
>
> Stage 4. A moss, *Rhacomitrium* sp., becomes important; the vegetation becomes mat-like and closed. *Cetraria* spp. (particularly *C. cucullata*) become abundant.

Stage 5. *Elymus* dies. Dead *Elymus* material persists (in the vegetation) for some time. *Cassiope tetragona* invades.

Stage 6. Mosses typical of moister sites (*Aulacomnium palustre* (Hedw.) Schwaegr. and others) appear. *Rhacomitrium* is invaded by *Hierochloe alpina* and *Poa arctica*.

Stage 7. Erosion often continues around the steep and uncolonized perimeter of such blowouts. In consequence, the adjacent surface is lowered and the protection afforded by snow accumulation is removed. In less protected areas, *Rhacomitrium* and *Cassiope* never appear, although *Hierochloe*, *Potentilla*, *Eritrichium*, *Silene* and *Minuartia* may be present. As the marginal erosion continues, blowout vegetation loses species associated with snow protection, and *Dryas* can invade and eventually form mats. Further wind erosion may undermine *Dryas*, and the cycle is reinitiated. Erosion may interrupt the cycle at any stage.

Elliptical blowouts with a variety of vegetational types can occur within even a small area. Occasionally, the slightly concave shape of a blowout bottom somewhat stabilized by a *Dryas* mat may be found perched above the surrounding surface. Increased soil moisture and decreased depth of thaw accompany the vegetational succession in these elliptical blowouts.

DISCUSSION AND CONCLUSIONS

It is clear from the results reported here that vegetational changes on the sandy bluffs of the Meade River result from a number of biotic and physical processes. The spatial patterns of vegetation not only provide the key to information concerning vegetational succession, but also reflect processes in the ecosystem. The role of spatial and temporal patterns in ecosystem structure must not be underestimated. Models of ecosystems and predictions of ecosystem behaviour based only upon population dynamics and trophic relationships of the constituent species in relation to environmental parameters are incomplete. The spatial and temporal interrelationships of species and habitats must be included if ecosystems are to be understood.

Geomorphic changes occurring on the bluffs act as trigger factors resulting ultimately in changes in soil moisture, depth of thaw, soils and vegetation. While geomorphic activity results primarily from climatic energy, biotic factors — e.g., vegetational stabilization of sands, disturbance by animals, and accumulation or decomposition of organic matter — may modify this activity. Geomorphic processes affect the vegetation primarily through the modification of topography. The influence upon vegetation of a change in topography may be direct, as in the case of sand deposition burying the moss layer of a bluff-edge community, or it may be indirect, as in the case of increased drainage of soils. Such drainage affects physiological performance and competitive interactions within the community.

The time scale of vegetational changes may be rapid (e.g., vegetational disturbance and blowout formation) or extremely slow (e.g., autogenic changes and changes resulting from soil formation). These latter changes take hundreds of years or more. Gradients in vegetational composition extending back from eroding bluffs are usually tens or hundreds of metres long, while bluff recession in active sites is estimated to have been one metre or less over the past 25 years. Autogenic succession seldom goes to an equilibrium (climax) condition on bluffs, due to continued animal and physical disturbances. However, autogenic succession appears to lead eventually to a lichen-heath vegetation type on well drained, protected bluff sites. This type is also often found along the gentle divides of the flat landscape. Mats of *Alectoria* spp. and the low evergreen shrubs *Diapensia lapponica*, *Vaccinium vitis-idaea* and *Ledum palustre* characterize this type. Soil development in such sites attests to the great length of time necessary for the establishment of this vegetational type. The time-scale of such vegetational succession is so long that future long-term successions may follow separate courses due to interactions with biotic migrations, climatic changes and evolution.

It is apparent that, even though this area essentially has been free of disturbance by man until now, the vegetation is constantly changing. In time, local vegetational types change through both autogenic and environmentally induced successions. Linear successions exist only within the framework of long-term cycles determined by geomorphic processes. Environmentally induced vegetational changes are common relative to autogenic changes on the Meade River sand bluffs due to the persistence of natural disturbances. Many potential vegetational sequences exist, and they are interrelated.

The stabilization of sand deposits in this part of the Arctic is facilitated by permafrost, which generally rises as vegetational cover increases. Mass-wasting and polygon-forming processes therefore can ultimately obscure dune forms. Patterned ground, on the other hand, is masked by sand deposition in many areas adjacent to bluffs. Where sand deposition is slight, bluffs may abut patterned ground. In such sites, the low-centre polygons commonly found in this region are replaced by high-centre forms at bluff edges.

Even though this ecosystem is characterized by natural disturbance to the vegetation, there is even greater potential for vegetational disturbance resulting from man's activities. The creation of new habitats or of new spatial habitat patterns (to which the community is not adapted) should be avoided to minimize the potential for deleterious effects upon the biota. As elsewhere in the Arctic, the potential for man-induced thermokarst erosion exists. In addition, there exists in this area the potential for man-induced aeolian erosion and deposition of sands, particularly in semi-stabilized sites. Once initiated, thermokarst and aeolian erosion may continue for long periods of time, with effects upon the vegetation spreading beyond the initially disturbed area. The potentially unstable nature of the sands of this region should be considered in plans for utilization of the region by people.

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