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THE VEGETATION OF SALT MARSHES AT SOME COASTAL SITES IN ARCTIC NORTH AMERICA

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SUMMARY

The vegetation of salt marshes was examined at seven sites on the Arctic coast of Alaska and Canada, at some of which measurements were made of the salinity of sea water, the amounts of standing crop of the vegetation and the distribution of biomass within plants. *Puccinellia phryganodes*, *Stellaria humifusa* and *Cochlearia officinalis* form the pioneer plant community on open coasts, but in sheltered bays and inlets, where vegetation cover is continuous, species such as *Arctophila fulva*, *Dupontia fisheri*, *Hippuris tetraphylla* and *Carex ramenskii* are frequent. The salinity of inshore sea water at most sites is very low. In this survey salinity values do not exceed 0·27 M Na^+ (*c.* 18‰). The total biomass for stands of the pioneer plants also is low (96–284 g m^{-2}). The above-ground:below-ground ratios of dry matter lie between 1:0·11 and 1:3·40. A tentative estimate of the net primary production of *Puccinellia phryganodes* indicates that a value of 10 g m^{-2} per annum appears to be an upper limit. The results are compared with similar data from Polar regions in North America and Eurasia.

INTRODUCTION

Polunin (1948) and Hanson (1951) have described the vegetation of coastlines in the eastern Canadian Arctic and western Alaska, and recently Kershaw (1976) has described some Hudson Bay salt marshes. Similar studies of the vegetation along the coastlines of northern Alaska and the western Canadian Arctic are scanty and information is confined largely to reports presented in the floras of the Arctic (Polunin 1959; Porsild 1964; Hultén 1968). This paper describes the vegetation at seven sites in northern Alaska and Canada (Fig. 1) and the results are compared with those obtained elsewhere in the Arctic. This preliminary study provides not only a description of vegetation but also data on prevailing salinities and amounts of standing crop at five of the sites. On open coastlines, marshes often occupy areas of less than 20 × 20 m and there is a discontinuous distribution of vegetation. Marshes which occur in sheltered bays and inlets, in contrast, are extensive and the vegetational cover is continuous. These latter sites are important feeding grounds for wildfowl. At most sites on open coasts, for example, Cape Bathurst, North West Territories and Point Barrow, Alaska, the marshes appear to be in an early stage of development, vegetational cover is poor and *c.* 80% of the shore consists of bare mud and sand devoid of higher plants. The shorelines are continually being reworked by sea ice during much of the year and, in addition, the tidal amplitude at many coastal sites in the Arctic is small; hence the influence of the tides in the formation of coastal marshes and in the development of vegetational zones within marshes is limited. The mean tidal range at Tuktoyaktuk, North West Territories, is only 0·305 m, while at Resolute, Cornwallis Island, *c.* 1700 km away, it is 1·28 m. The estuaries of the large number of rivers

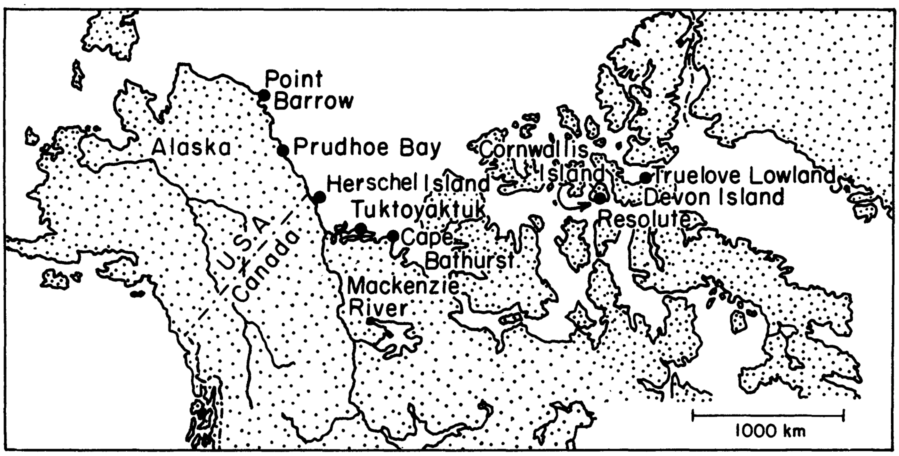

FIG. 1. Map showing the location of coastal sites which were examined in Arctic North America.

which flow into the Arctic Ocean are an important physiographic feature of the coastline and large quantities of gravel, sand, silt and clay are deposited in the vicinity of these estuaries.

The physical characteristics of coastlines described above preclude the long term development of salt marshes on open coasts.

METHODS

With the exception of the sites at Resolute Bay, Cornwallis Island and Herschel Island, North West Territories, where only notes on the vegetation were made and samples collected, the vegetation was recorded along transects which were oriented perpendicular to the shore line, running from near the prevailing low water mark to a point well above the high water mark of the highest tides. Contiguous quadrats were placed along each transect and the percentage cover contributed by each species was estimated subjectively to the nearest 10%. The size of the quadrat (30 × 30 cm, 50 × 50 cm or 100 cm × 100 cm) was selected subjectively in relation to the pattern and type of vegetation observed at a site (cf. legends to Figs 2, 3 and 4). The taxonomic nomenclature follows that of Porsild (1964) for vegetation in the eastern Canadian Arctic and Hultén (1968) for the western Arctic.

In order to measure the distribution of dry matter between different organs of plants, five turfs (25 × 25 cm in area and 35 cm in depth) were selected at random at a site and transported to the field laboratory. Plants in the centre of the turfs were separated into above-ground living material, standing dead litter and below-ground material. Living material was further subdivided where applicable into leaves, stolons, and sexual reproductive organs. The below-ground biomass was separated into rhizomes and/or roots. Initially the samples were air-dried but subsequently they were oven-dried at 80 °C before they were weighed. At least five plants of the species examined at each site were dried and weighed.

At many sites the distribution of vegetation on the foreshore is markedly heterogeneous and extensive sampling was not possible at these remote sites. However, biomass estimations were made between 15 July and 10 August 1973 in areas of vegetation which were composed of a single species and through which a transect line passed. Five 20 × 20 cm turfs were cut at random within these areas. The material was separated into leaves, reproductive organs, standing dead and ground litter of the component species, and then dried and weighed as described above. The ratios of the distribution of dry matter within plants of each species were used to obtain an estimate of the below-ground biomass.

In order to obtain information on the salinity of these coastal waters, water from below the tide line was collected in polythene bottles during the same period of time and stored at 2 °C. At each site duplicate samples were taken. At a later date the concentrations of sodium, potassium, calcium and magnesium in the waters were measured by atomic absorption spectrophotometry and no differences in salinity between duplicate samples were recorded.

RESULTS

Salinity

Although the results of the analysis of the water samples (Table 1) are based on a single set of samples collected during a short period of time, they reflect the salinity regimes which exist during the active phase of plant growth. At no locality did the salinity approach that usually quoted for sea water (*c.* 0·5 M sodium). At sites such as those at Tuktoyaktuk the salinity was extremely low ($2{\cdot}9 \times 10^{-2}$ M sodium) and it was only at sites away from the influence of large rivers such as at Herschel Island and Cape Bathurst that higher salinities were recorded (0·25 M and 0·1 M sodium respectively). Even at these sites the melting of sea ice lowers the salinity of the water. Grainger (1965) has reported that at inshore sites along the southern edge of the Beaufort Sea, summer surface temperatures may reach 9 °C and the salinity is usually less than 10‰ (*c.* 0·15 M sodium). There is a wedge of fresh or brackish water which lies above the sea water during the summer months at these inshore stations.

The marshes receive, in addition to sea water, drainage water from the surrounding

Table 1. *Latitudes and longitudes of six study sites and the ionic concentrations of major ions in samples of inshore coastal water collected between* 15 *July and* 10 *August* 1973

	Latitude	Longitude	Ionic concentrations (mM)			
			Na	K	Ca	Mg
Truelove lowland,	75°40′N	84°40′W	1·2	0·01	0·9	2·0
Devon Island,			3·1	0·04	2·2	4·1
North West Territories*			3·8	0·05	1·3	3·8
			50·0	0·20	1·3	4·7
			23·0	0·15	1·8	4·5
Cape Bathurst, N.W.T.*	70°34′N	128°00′W	100·0	1·00	4·6	24·0
			100·0	1·00	4·6	25·0
Tuktoyaktuk, N.W.T.*	69°27′N	133°00′W	29·0	0·23	1·3	12·0
			28·0	0·25	1·0	12·0
			33·0	0·25	0·8	14·0
			28·0	0·20	0·9	11·0
Herschel Island, N.W.T.*	69°34′N	138°55′W	250·0	1·75	7·0	50·0
			270·0	2·00	7·0	50·0
Prudhoe Bay, Alaska	70°19′N	148°19′W	72·0	0·58	4·0	15·0
Point Barrow, Alaska	71°18′N	156°34′W	134·0	1·08	6·2	34·0

* Where more than one value of the concentration of an ion is given for a locality it indicates samples were collected from different sites.

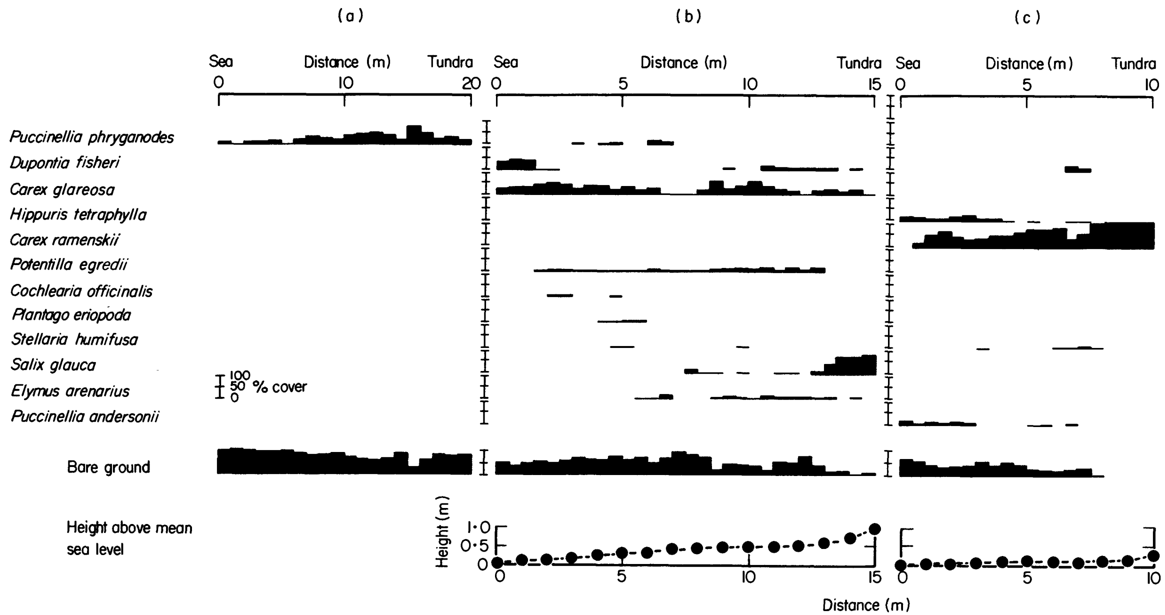

FIG. 2. The percentage cover values of the plant species on transects at three sites on the shores of the Arctic Ocean in the region of the Mackenzie Delta: (a), Cape Bathurst (quadrats all 100 × 100 cm); (b) and (c), Tuktoyaktuk Sites A and B (quadrats all 50 × 50 cm).

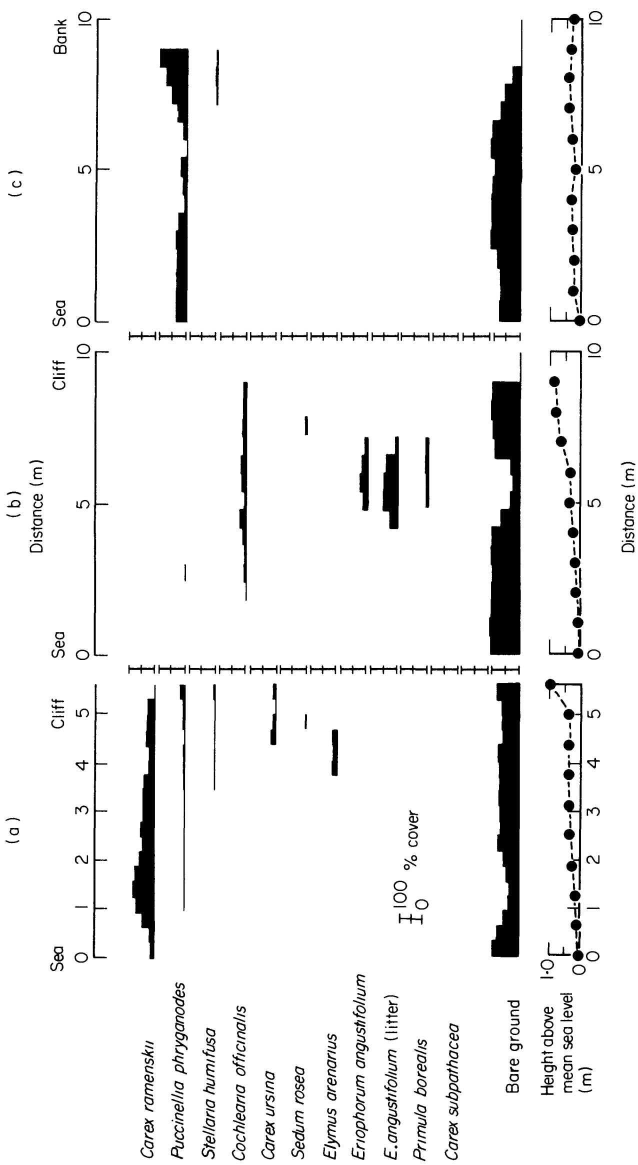

FIG. 3. The percentage cover values of the plant species on transects at three sites on the shores of the Arctic Ocean in northern Alaska: (a), Prudhoe Bay Site A (all quadrats 30 × 30 cm), (b), Prudhoe Bay Site B (all quadrats 50 × 50 cm); (c), Point Barrow (all quadrats 50 × 50 cm).

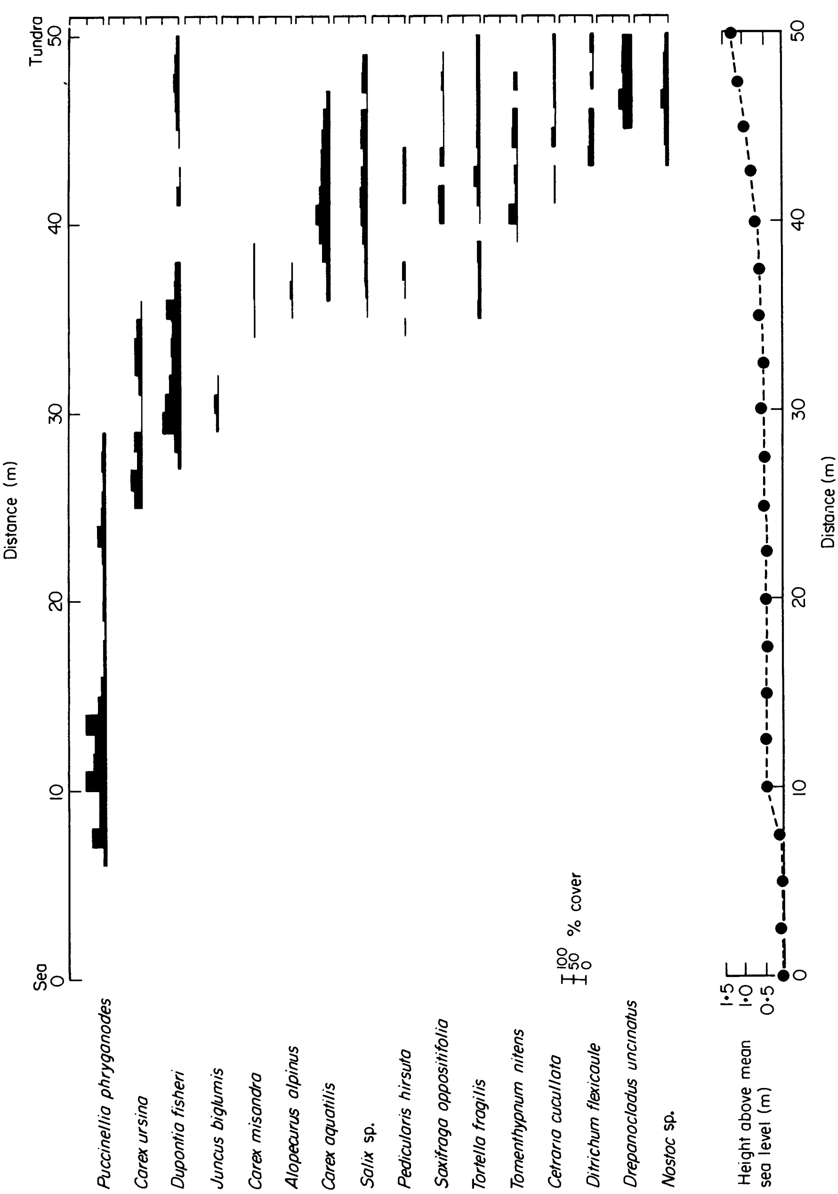

FIG. 4. The percentage cover values of the plant species along a transect at a coastal site on the Truelove lowland, Devon Island; each quadrat was 100 × 100 cm in size.

land. The low salinities recorded at Devon Island ($3{\cdot}1 \times 10^{-3}$ M sodium) reflect the transition from salt to fresh marsh.

Description of vegetation

Puccinellia phryganodes is the first angiosperm to colonize open muddy and sandy areas at all the sites (Figs 2, 3 and 4). Polunin (1940) has stated that the species is also an important colonizer of mud flats in the eastern Canadian archipelago. Plants of this species undergo clonal reproduction and the stolons grow across the surface of muddy shores. Often the plants are yellow-brown and stunted but where they are partially covered by a decaying algal mat left by a high tide growth is vigorous and the plants are green. This suggests that nutritional deficiencies restrict growth. In some European salt-marshes, for example, the lack of the availability of nitrogen may restrict the growth of plants (Tyler 1967; Pigott 1969; Stewart, Lee & Orebamjo 1972, 1973).

Puccinellia phryganodes rarely flowers and apparently at Arctic coastal sites in both Eurasia and North America plants which flower do not set seed (Holmberg 1926; Polunin 1940; Sørensen 1953; Porsild 1964; Hultén 1968). Only at the upper levels of marshes where the plants are rarely or not at all submerged by sea water does the plant form cushions which may bear flowering culms. This confirms Porsild's (1920) earlier observation.

In addition to *Puccinellia phryganodes*, *Stellaria humifusa* and *Cochlearia officinalis* agg. are present at the seaward end of most marshes (Figs 3 and 4). Although these two species occur in saline sites in the Arctic, they are not restricted to this type of habitat. For example, on Cornwallis Island both grew at least 2 km from the coast at the edge of a seepage zone associated with *Saxifraga cernua*, *S. oppositifolia* and *Papaver radicatum*. At Prudhoe Bay, Alaska, *Cochlearia officinalis* ssp. *arctica* has colonized bare areas of tundra devoid of vegetation. These areas were flooded by sea water during a storm in 1969 and the plants subsequently died. With the exception of plants from Devon Island all the material appeared to be *Cochlearia officinalis* ssp. *arctica*. The plants from Devon Island were much smaller (*c.* 1·5 cm in diameter) than those from the coastal sites of the western Arctic (3–8 cm diameter) and belonged to ssp. *groenlandica* (Porsild 1964).

Primula borealis and *Carex ursina* also grow in salt-marshes where the vegetational cover is small, although these species are not found at the seaward ends of the foreshores. Porsild (1955) considers that *Primula borealis* is a member of a group of species characteristic of east Siberia. In the present study, this species was not observed east of the Mackenzie Delta, although at Tuktoyaktuk, Herschel Island and Prudhoe Bay, it grows at the base of earth cliffs or on tundra in close proximity to the shore. *Carex ursina* is common to both the western and eastern Arctic (Figs 3 and 4) and in contrast to the species discussed above, plants of this species have a well-developed caespitose growth habit so that individual tussocks may be of considerable age. The other species are either biennials or short-lived perennials. Both *Primula borealis* and *Carex ursina* grow in sites which are relatively well drained whereas *Puccinellia phryganodes* and *Stellaria humifusa* grow in sites where surface water often is present.

At Tuktoyaktuk Site A (Fig. 2) where there was a considerable amount of gravel and sand, other species such as *Elymus arenarius* ssp. *mollis* var. *villosissimus*, *Armeria maritima* ssp. *arctica*, *Juncus arcticus* ssp. *alaskanus*, *Plantago eriopoda* and *Honkenya peploides* ssp. *peploides* grew above the level of the tides in the vicinity of the transect. Two of these species, *Elymus arenarius* and *Honkenya peploides*, are more characteristic of strand vegetation than salt marsh plant communities.

In sheltered bays and inlets where the shoreline is stable the ground is usually completely covered with vegetation and, depending on the state of the tide, the plant communities may be flooded much of the time. At sites near Tuktoyaktuk where the salinity is low and brackish conditions prevail (cf. Table 1 and Fig. 2) species characteristic of the coastal freshwater lagoons grow along the sea shore. For example, *Arctophila fulva*, *Dupontia fisheri* and *Hippuris tetraphylla* were found growing in the sea. The dominant species of this type of marsh is *Carex ramenskii* (Fig. 2) which forms lush swards. The closely related species, *C. subspathacea* is restricted to areas of bare mud where secondary erosion has occurred. Another sedge, *C. glareosa*, is found in similar sites in the upper reaches of marshes, above the normal high water mark of tides. With the exception of plants of *Puccinellia andersonii* and *Calamagrostis neglecta* and some plants of *Stellaria humifusa*, other species of higher plants are absent amongst the swards of *Carex ramenskii*.

These plant communities are important feeding sites for migratory populations of eider (*Somateria mollissima L.*), pintail (*Anas acuta L.*), mallard (*Anas platyrhynchos L.*), and old squaw (*Clangula hyemalis L.*).

Determinations of biomass

Although these measurements are based on samples collected at one point of time at a site, they were made during the period of the year when the standing crop of the tundra is either at or close to its peak.

Values for total biomass for stands of *Puccinellia phryganodes* at the different sites are between 96 and 284 g m^{-2} (Table 2) and these represent some of the lowest values obtained for biomass within the Arctic. Habitats where there is no continuous cover of vegetation have similar values. Polar desert sites in the U.S.S.R., lichen heath and snow bed habitats in Norway and beach ridges on Devon Island, Canada, are other examples where the total living biomass per unit area is low (Wielgolaski 1972).

Where the vegetational cover is continuous, higher biomass values were recorded. The communities of *Carex ramenskii* at Tuktoyaktuk had a biomass of 445±251 g m^{-2} while the biomass of stands of *Dupontia fisheri* on Devon Island was 332±29 g m^{-2}

Table 2. *The dry weight of the living parts* (*g m^{-2}±s.e.m.*) *at or near the time of peak above-ground standing crop* (*samples collected* 15 *July*–10 *August* 1973)

	Site	Above-ground biomass	Below-ground biomass	Total
Grasses				
Dupontia fisheri	Devon Island	61·4± 5·4	270·6± 23·8	332·0± 29·2
Puccinellia phryganodes	Devon Island	86·4± 5·8	82·7± 5·6	169·1± 11·4
P. phryganodes	Cape Bathurst	77·5±32·9	63·7± 27·6	141·2± 46·6
P. phryganodes	Herschel Island	56·5	102·5	159·0
P. phryganodes	Point Barrow	145·1	138·8	283·9
Sedges				
Carex ramenskii	Tuktoyaktuk	155·7±89·4	289·5±161·2	445·2±250·6
C. subspathacea	Point Barrow	94·2	178·8	273·0
C. ursina	Devon Island	120·9±16·7	229·3± 31·8	350·2± 42·5
C. ursina	Herschel Island	67·7	143·7	211·4
Eriophorum angustifolium	Prudhoe Bay	13·5	25·7	39·2
Dicotyledon				
Stellaria humifusa	Point Barrow	72·5	45·2	117·7

Table 3. *The distribution of dry matter within selected plants, expressed as a percentage of the total dry weight (±s.e.m.) and the ratio between above-ground and below-ground dry weight; values in parentheses are combined dry weights of the parts bracketed (expressed as a percentage of the total dry weight)*

Species and number of samples	Site	Leaves	Stems	Inflorescences	Rootstock or rhizomes	Roots	Dead leaves	Ratio of above-ground to below-ground dry weight
Grasses								
Dupontia fisheri (5)	Tuktoyaktuk	18·3± 5·1	(4·38±0·7)		31·5± 7·3	38·8 ±18·0	7·07± 3·19	1:3·40
Puccinellia phryganodes (5)	Cape Bathurst	(54·9±22·3)				45·1 ±19·6		1:0·82
Sedges and rushes								
Carax ramenskii (5)	Tuktoyaktuk	25·7± 6·3	(1·85±0·03)		46·3±13·5	6·11± 2·71	20·0 ± 6·9	1:1·90
Juncus arcticus (5)	Tuktoyaktuk	22·6± 4·5			38·6±13·7	2·06± 0·58	36·8 ±15·6	1:1·80
Dicotyledons								
Armeria maritima (5)	Tuktoyaktuk	29·8±12·6		20·5±16·2	(27·6±8·1)		22·2 ±13·8	1:0·55
Cochlearia officinalis ssp. *arctica* (5)	Prudhoe Bay		(90·1±6·5)			9·90± 0·51		1:0·11
Cochlearia officinalis ssp. *groenlandica* (10)	Devon Island		(72·9±11·7)			27·1± 2·0		1:0·37
Plantago eriopoda (5)	Tuktoyaktuk	27·9±10·2		13·1± 4·8	23·5± 9·3	35·5 ± 8·4		1:1·45
Potentilla egredii (5)	Tuktoyaktuk	38·8± 3·2	14·1±6·7	8·6± 2·9		38·5 ± 4·9		1:0·63
Primula borealis (6)	Prudhoe Bay	82·1± 7·0	(12·2±4·5)			6·47± 4·12		1:0·06
Stellaria humifusa (5)	Tuktoyaktuk	(79·0±4·5)		10·9± 5·5		10·1 ± 0·9		1:0·11

(Table 2). These values are comparable with those for other wetland sites in the Arctic with a continuous cover (Wielgolaski 1972).

The percentage distribution of dry matter between the above-ground and below-ground portions of plants of different species are given in Table 3. The above-ground:below-ground ratios are not as low as those provisionally quoted for some Arctic communities where the ratio may be as low as 1:23 but usually it lies between 1:3 and 1:10 (Wielgolaski 1972). The relatively large ratio of above-ground biomass to below-ground dry matter reflects the growth habit of plants which live in this narrow coastal strip. They are either short-lived perennials or monocotyledonous plants with a rhizomatous or stoloniferous habit where individual tillers may live for a few years. K. Bell (private communication) has estimated the growth rates of plants of *Puccinellia phryganodes* at different sites in the Arctic and her results indicate that between one and two leaves are produced by each tiller per year. The leaves are relatively short-lived as only 20% of the tillers had living leaves more than two years old. Individual tillers are approximately eight years old, an estimate which is based on the number of dead leaves along the entire length of each tiller. If the above-ground living biomass for this species is assumed to be 80 g m^{-2} (Table 2), a value for net primary production of 10 g m^{-2} per year appears to be the upper limit for stands of *P. phryganodes*.

In addition to the low net productivity of these pioneer seashore communities, there is a paucity of species. Although this is well known for terrestrial plant communities in the Arctic, it is particularly striking in these coastal sites. Annuals, such as species of *Salicornia*, *Spergularia* and *Suaeda*, present in temperate salt marshes, are absent in the Arctic. Certain well-known salt marsh perennials, such as *Triglochin* and *Limonium*, have not been recorded from the foreshores along the Arctic Ocean. Most of the above genera are represented in coastal marshes in southern and western Alaska (Hanson 1951; Hultén 1968) and *Triglochin palustris* grows in Hudson Bay (Kershaw 1976).

DISCUSSION

There is a striking uniformity of the pioneer plant communities present on the seashore at the different sites. *Puccinellia phryganodes* and *Stellaria humifusa* are widespread. The former species occurs both in the North American Arctic and in the Arctic areas of Eurasia (Sørensen 1953). It shows considerable variation throughout its range and Sørensen has distinguished four races based on morphological characters, and one of these is characteristic of the North American Arctic. As Sørensen points out, the wide distribution of *P. phryganodes* is of interest, as the plant fails to set seed and therefore spreads as a result of vegetative reproduction. The shoot systems must be capable of tolerating low temperatures and considerable periods immersed in sea water. Both this grass and the *Stellaria* are able to colonize a variety of substrata. They grow on sandy shores and where mud predominates. At the Truelove lowland on Devon Island, both species occur in small rocky pools which are well above the level of the tides and which are fed by ice-melt water.

Puccinellia andersonii and *P. vaginata*, which are present also in the coastal zone, occur at sites well above the high water mark of the tides, but their distribution is local. Sørensen (1953) has suggested that, at least in the eastern Canadian Arctic and Greenland, the distribution of *P. vaginata* may reflect the influence of man, as the Inuit (Eskimos) used the straw of this grass in basket-making. Hence the reasons which account for the present distribution patterns along the coastlines are probably complex. The pioneer communities are transitory and no long-term development of these incipient salt-marshes appears to have taken place except in sheltered sites (e.g. Truelove lowland, Devon Island and at Tuktoyaktuk). As a result it is not usually possible to recognize vegetational zones in the Arctic and place them in sequence, as Hanson (1951) has done for the marshes of western Alaska and Chapman (1960) has done for those of north-west Europe. Rather, there is a vegetational mosaic in these narrow sea-shore strips which at any given site reflects the time which has elapsed since the shore was re-worked. This physical instability also implies that pedogenetic long-term development, which is clearly evident at coastal sites in more southerly latitudes (Gray & Bunce 1972) and is strongly dependent on past and present edaphic and biotic conditions, is checked. Where zones of vegetation are clearly recognizable (e.g. Truelove lowland, Devon Island, Fig. 4) they reflect a transition from saline or brackish water conditions to fresh-water conditions and not the development of different plant communities within a saline environment.

The coastal vegetation described in this paper is similar to that reported by Polunin (1948) and Chapman (1960), for the eastern Canadian Arctic, Greenland and northern Europe. In salt marshes on Ellesmere Island, Devon Island, North Baffin Island, the Melville Peninsula and northern Quebec, *Puccinellia phryganodes* and *Stellaria humifusa* are present and in most of these sites *Cochlearia officinalis* and *Carex ursina* also grow (Polunin 1948). Around Hudson Bay, the primary community consists of *P. phryganodes* and *Stellaria humifusa*. In Finmark, Norway (Nordhagen 1954), this grass colonizes the open shore and in both Canadian and Norwegian Arctic sites *Carex subspathacea* is present above the high water mark (Chapman 1960). At Tuktoyaktuk *Carex glareosa* grows in the upper levels of the marsh and Chapman reports a similar distribution of this species in the White Sea and Greenland marshes. Even though many of the above studies are preliminary, they indicate a considerable similarity in the composition of the vegetation of salt marshes in polar regions.

The plant biomass data are based on a single collection and they overestimate the below-ground living material as tissue was not differentiated into living and dead. The error is likely to be small as unlike the woody, long-lived perennial plants of the tundra which have much of their biomass below ground and accumulate large quantities of below-ground litter, the forbs and some of the monocotyledons such as *Puccinellia phryganodes* are short-lived perennials with poorly developed below-ground storage organs, but capable of colonizing open habitats. The ratio of above-ground to below-ground biomass is least for the forbs and relatively high for the sedge-dominated communities (Table 3). These results agree with those reported by Wielgolaski (1972).

Although the estimate of net primary production for *P. phryganodes* communities of under 10 g m^{-2} per year needs substantiating it implies that the productivity of this type of community is extremely low. The only other sites with similar measured values are lichen heath in Norway (9 g m^{-2} per year above-ground net production) and polar semi-desert in the U.S.S.R. where the corresponding figure is 26 g m^{-2} per year (Wielgolaski 1972). All these sites are open and with little cover of vascular plants.

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