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Phytosociology and Succession on Earthquake-Uplifted Coastal Wetlands, Copper River Delta, Alaska

John F. Thilenius

Author

JOHN F. THILENIUS was a research wildlife biologist (now retired), Pacific Northwest Research Station, Forestry Sciences Laboratory, P.O. Box 20909, Juneau, Alaska 99802-0909.

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Abstract

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The delta formed by the Copper River stretches more than 75 kilometers along the south-central coastline of Alaska. It is the terminus of the outwash deposits from a large part of the most heavily glaciated region of North American, and all major rivers that flow into the delta carry extremely high levels of suspended sediments. Coastal wetlands extend inland for as much as 20 kilometers. In 1964, an earthquake of Richter Scale 8.4 to 8.6 raised the entire delta from 1.8 to 3.4 meters above the previous mean sea level. Subtidal areas became intertidal, and intertidal areas supertidal. Marshland advanced seaward as much as 1.5 kilometers in the intertidal zone. Vegetation on many, but not all, newly supertidal levees began to change from herb to shrub. A change in frequency and duration of tidal inundation and water salinity has been thought to be the most obvious cause of this succession, but explanation is lacking. Fresh water dominates the estuarine circulation as a result of a bar-built estuary and the extremely high input of fresh water from glacier runoff and precipitation. Tides merely raise fresh water onto the wetlands. Halophytes are rare even at the seaward edge of vegetation. The characteristic species of the present intertidal marshes, *Carex lyngbyei*, also is characteristic of inland freshwater marshes. Initial postearthquake invasion of woody plants was confined to natural levees. More recently, shrubs have begun to move seaward into new intertidal marshland and into supertidal interlevee basins. Current plant communities on new marshland (tidal) are *Carex* C-T (low marsh); *Carex* C-T (high marsh); *Carex/Potentilla* C-T (low levee); and *Myrica/Carex-Potentilla* C-T (high levee). On old marshland (nontidal) the current plant communities are *Alnus/Myrica-Salix/Carex* C-T (foreshore levee); *Myrica/Carex-Calamagrostis* (foreshore levee); *Carex/Equisetum-Lathyrus* C-T (interior levee); *Carex/Lathyrus* C-T (moderately hydric interlevee basin); and *Carex-Cicuta*/C-T (hydric interlevee basin). Vegetation analogous to that developing on supertidal levees and basins is present on older wetland habitats further inland. Likely, the same plant successions would have occurred without an uplift. The uplift appears to have altered locations and rates, but not the nature, of wetland plant succession on the Copper River Delta.

Keywords: Copper River Delta, plant ecology, plant succession, tidal marshlands, tectonic uplift, Alaska.

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Introduction

The Copper River Delta is a vast (about 28 300 hectares), remote, and generally inaccessible area along the south-central coast of Alaska between 60° and 60°30' N. latitude and 144° to 146°30' W. longitude. It contains the largest contiguous area of coastal wetland on the Pacific Coast of North America (fig. 1).

In 1964, an earthquake registering 8.4 to 8.6 on the Richter scale occurred in the gulf coast region of south-central Alaska (Hansen and Eckel 1971). The epicenter was about 130 kilometers northwest of the mouth of the Copper River, but the entire river delta, including the estuary, was uplifted enough (1.0-4.0 meters) to completely change the tidal regime of the wetlands. Subtidal areas became intertidal, and intertidal areas became supratidal.

One result of the uplift was a seaward extension of tidally influenced, sedge-dominated marshland. In places, new marsh now occupies tidal flats as much as 1.5 kilometers seaward of the foreshore levee that defined the outer edge of the preearthquake marshland. The wetlands inland from the foreshore levee (hereafter called old marsh) were no longer occasionally inundated by tidal water, although portions of them still may be flooded by silt-laden glacial runoff water and by water from rainfall or snowmelt.

On the old marshlands, an alteration of the physiognomy of the vegetation from herbland to shrubland was noted soon after the earthquake (Crow 1971, Olson 1964, Shepard 1964). Most of this successional development seemed to have occurred on the slightly higher elevation natural levees, which parallel major river courses and distributary stream channels throughout the old marshland and on the foreshore levee mentioned above. Willows (*Salix* spp.) apparently were the most easily seen shrub, because the term "willow invasion" was used to describe the structural change in the vegetation.

Resource managers concerned with the wildlife populations of the Copper River Delta were pessimistic that this successional change would deteriorate the value of the wetlands as wildlife habitat. Unfortunately, little qualitative and no quantitative information was available on the nature of the preearthquake vegetation, and as the entire region had been uplifted, a quantitative reference base or untreated control was unavailable. Quantitative information on the wildlife populations also was unavailable.

The purposes of this study were:

1. To quantitatively determine the phytosociological units of marshland vegetation that have developed in the Copper River Delta since the 1964 uplift.
2. To relate the current phytosociological units of vegetation to habitat and environment.
3. To describe the nature of the preearthquake marshland vegetation and clarify some possible misconceptions commonly held about this vegetation, its successional development, and its relation to the current vegetation.

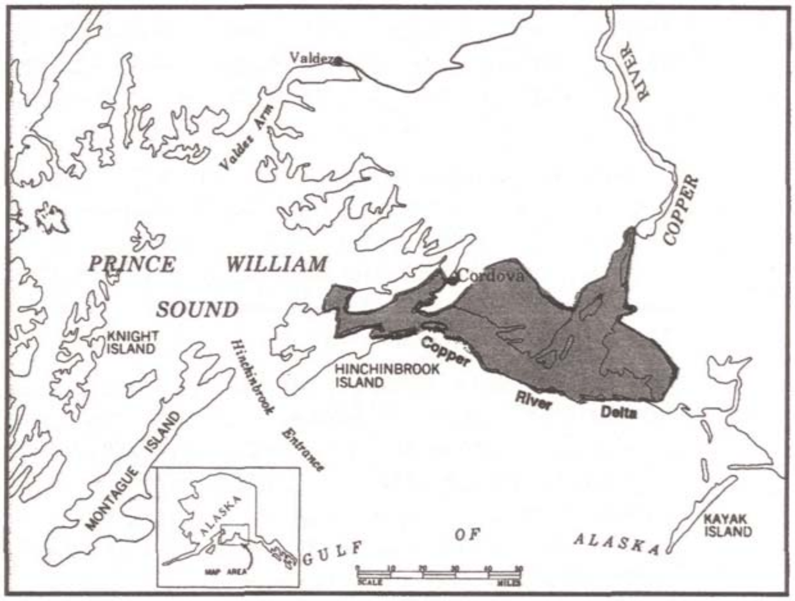

Figure 1—The wetlands of the Copper River Delta.

The Copper River Delta

Tectonics and Stratigraphy

The 1964 earthquake was the most recent of at least five similar coseismic uplifts of 2 to 3 meters each that have occurred in the last 3000+ years (Pflaker 1990). The mean intervals between previous uplifts were about 790, 670, 950, and 600 years. There is no record of coseismic subsidence, but the stratigraphy indicates that in the intervals between uplifts, interseismic submergence (tectonic subsidence plus rise in eustatic sea level) exceeds coseismic uplift. However, the extremely high rate of deposition of glacial sediments from the Copper River and several smaller rivers flowing from local glaciers causes an accumulation of sediments on the delta that is about equal to the rate of submergence (Reimitz 1966).

This repetition of uplift, subsidence, and sedimentation is reflected in the stratigraphy; there are several layers of peat derived from intertidal and freshwater marshes, shrub swamp, and at least two buried coniferous forests of *Picea sitchensis*. The relics of past vegetation are interbedded with fine sediments from tidal deposits and coarse sediments from glacial meltwater floods.

Physiography and Substrate

The large-scale physiographic zones of the western Copper River Delta are offshore sandy barrier islands, estuarine tidal flats, marshlands, glacial outwash plains and piedmonts, and coastal mountains. The outwash plains and marshland are crossed by the braided channels of rivers flowing directly from local glaciers and by several major distributary channels of the Copper River. These watercourses usually have sufficient flow to cut more or less permanent channels across the estuarine tidal flats, but the actual geographic location changes over time as a result of erosion and deposition. Channels, small rivers, and drainage creeks usually merge gradually into the tidal flats.

Sand dunes to 90 meters in elevation are present along the Copper River as islands in its 20-kilometer-wide braided channel. Both active and stable (vegetated) dunes are present. The sand dunes and the sandy barrier islands represent completely different ecosystems from the wetlands and as such are worthy of separate study. No scientific information is presently available for these ecosystems.

The vegetated portion of the tidal flat zone has four distinct small-scale topographical features: levees paralleling the channels of rivers and streams, scattered small islands of organic material, sandy low mounds and ridges, and pans.

Levees are the result of differential deposition of suspended inorganic sediments, organic detritus, and living organisms from tides and runoff water overflowing the banks of the channels. Deposition is due to a change from laminar flow to turbulent flow and is greatest next to the channel. The levee consequently accretes at a greater rate than areas further from the channels. Because of this, the levee is where the initial colonization by vascular plants takes place. Colonization by vascular plants further increases the rate of sediment deposition and surface accretion (Ranwell 1972).

The organic islands are pieces of water-transported riverbank. Large blocks of riverbank often break off after being undercut by water. These blocks are high in organic material and consequently of low density and readily transported by water. Such blocks, with their vegetation intact, ground on the tidal flats. If not too far into the subtidal zone, the blocks may gradually become part of the tidal flat surface. The vegetation on the block persists, and small islands of old marsh vegetation may occur several hundred meters out on the tidal flats.

Sand mounds and ridges are the result of the grounding of an ice floe that has accumulated sand on its lower side. The sand comes from the bottom of the channels of the major rivers. Ice floes move downstream, ground temporarily in the channels at low tide where sand freezes to the underside, are refloated by high tides, and eventually ground on the tidal flats where they melt. Mounds and ridges up to 0.3 meter deep and several meters in diameter or length are not uncommon. The well-drained sand mounds are rapidly occupied by plants growing on the immediately adjacent marshland.

Pans, more or less circular and shallow concave surface depressions, are a distinct terrain feature of the tidal flats near the outer edge of the vegetated zone. Pans often are found at the heads of small drainage channels that are extending inland through headcutting erosion. The substrate of a pan is very tightly packed glacial silt, and water does not seem to readily infiltrate. The most seaward pans are almost bare of vegetation but more inland pans may have a sparse to moderately dense vegetation cover. Pans also may be an initial stage in the development of wetland ponds.

The boundary between the new marshland and old marshland zones is defined by a 1- to 2-meter-high foreshore levee, located at about the mean higher, high tide level. The steep outer edge of this foreshore levee is a wave-cut terrace. The foreshore levee is almost continuous along the entire boundary except where cut by rivers and distributary creeks. It is from only a few meters to over 20 meters wide.

The old marshland inland of the foreshore levee also has distinct, small-scale physiographic zonation. From the channel of a watercourse, the terrain zones are water channel, steeply sloping lower channel bank, berm, less steep upper channel bank, levee, and interlevee basin.

The steep Iower channel bank is mostly unvegetated mud. Where it is within reach of tidally uplifted water, a can be partially inundated twice a day. The berm is a watercut terrace formed by current action and is located at about mean higher high water. The channel bank above the berm usually is well vegetated. It can be flooded only by the highest spring tides but may receive continuous lateral drainage water from the interior of the marsh and surface runoff water from the levee. Seeps are common along the upper channel bank, and lateral erosion rills are abundant along the channel edge of the levee. The channel levee is of depositional origin and has an almost level surface and the highest elevation of all the physiographic features of the old marsh. Before the uplift in 1964, more seaward channel levees were occasionally flooded by extremely high spring tides, especially when these were accompanied by storm surge. This flooding has not occurred since the uplift, but channel levees still may be flooded for short periods during heavy precipitation events.

Channel levees and foreshore levees are much alike. Both are of depositional origin, are well vegetated, have a species-rich vegetation, and have reasonably well-drained surface soils with distinct horizons and ped structure.

Channel levees are almost flat; the foreshore levee has a more undulating surface topography and soiIs that tend to be sandier. The greater sand content may be caused by frequent floodings and increased wave action during formation and by the melting of grounded ice floes (previously described). Foreshore levees also have more driftwood and other transported material incorporated into the surface than do channel levees. Along the landward edge, both types of levee slope very gradually into the interlevee basin zone.

The interlevee basin has the largest area of any of the old marsh physiographic features. Because of the dense vegetation and general lack of decomposition, the surface substrate of the basin is organic. Glacial silts and other inorganic substrates are found only at depths of 1 meter or more. The water table is at or above the surface throughout the growing season. The interlevee basins were occasionally flooded by tidal water before the uplift, but this no longer occurs. Direct flooding after intense precipitation and from river overflow still occurs. Interlevee basins have almost flat topography, but the local surface may be undulating due to tussocks and accumulation of organic material.

Scattered throughout the interlevee basin are numerous eutrophic freshwater ponds. The ponds rarely exceed 0.7 meter in depth and range from a few centares to several hectares in area. The ponds have been formed by various geological and biological processes. In the more seaward interlevee basins, many of the ponds have vegetation only around the banks. Further inland, floating and emergent plants are more common. Many of the most inland ponds are in floating mat or anchored mat stages of advanced hydrosere succession.

Tidal Regime

The extreme range of the tide is from -0.9 to 4.3 meters; the mean is 1.7 meters. During the May-October period, the tidal water flooding the new marsh is almost fresh or very low in salinity. There are several reasons for this. First, the Copper River system has about one-sixth of the flow of the Missouri-Mississippi River system. This enormous freshwater plume floats on the surface of the ocean offshore from the Copper River Delta because fresh water is less dense than salt water. Prevailing currents along the shore, wind direction, and Coriolis force turn the plumes westward, and the surface water several kilometers seaward of the barrier island thus has relatively low salinity. In addition, a large input of fresh water directly into the estuary from three local glaciers further dilutes the salinity of the estuarine water. Second, 60 percent of the total annual precipitation falls as rain during the May-October period. Cloudy weather predominates during summer so that, although the daylight period is long, direct insolation is low, relative humidity is high, and evaporation is minimal. Third, because the uplift raised the entire area, the low-salinity water of the tidal wedge now reaches the surface 2 to 2.5 kilometers seaward of the foreshore levee. Most of the vegetated portion of the tidal flats is within 1500 meters of the foreshore levee.

Climate

No climatic data are available for the Copper River marshlands. The closest and most appropriate weather station is at the Cordova airport, 9 kilometers inland (60°30’ N. 145°30’ W., elevation 12.2 meters). Mean yearly climatic attributes for the Cordova airport are temperature, 3.7 °C; precipitation, 251 centimeters; snowfall, 322 centimeters; wind speed,7.8 kilometers/hour; prevailing wind direction, east; and number of cloudy days per year, 262 (U.S. Department of Commerce 1979a, 1979b). The wettest months are September (39.3 centimeters) and October (39.5 centimeters). December is the coldest month (-3.9 °C) and has the most snowfall (74.9 centimeters). Sky condition and precipitation for the May-to-September growing period are given in table 1.

Table 1—Mid-month day length, sky conditions, and precipitation for the coastal area off Cordova, Alaska, May to September

Condition	May	June	July	Aug.	Sept.	$\bar{x}$	se
Day length at mid month (hours)	17.2	19.9[a]	18.1	15.2	12.7	16.6	2.8
Sky overcast or obscured (percent of month)	49.0	53.8	62.3	46.9	43.9	51.2	7.2
Mean cloud cover (percent of sky covered)	76.3	82.5	85.0	76.3	76.3	79.3	4.2
Fog (percent of month)	25.8	36.7	54.8	45.2	36.7	39.8	10.8
Precipitation (days per month)	23	22	24	23	22	22.8	0.8
Mean precipitation (milimeters)	152	119	180	227	334	202	83.6

[a]Sunrise to sunset period at solstice is 20 hours.
Source: U.S. Department of Commerce 1979a, 1979b.

Vegetation

The most abundant and widely distributed plant in the marsh is *Carex lyngbyaei*.[1] It grows as individual shoots, in tussocks and ring-shaped formations (clones), and in dense meadows. The most luxuriant stands are on the levees bordering tidal creeks where culms of *C. lyngbyaei* may exceed 1 meter in height. There appear to be two growth forms (ecophenes) of *C. lyngbyaei* similar to those described by Jefferson (1975). Associated with *C. lyngbyaei* at the outer edge of the low marsh is a very sparse cover of *Puccinellia phyrganodes* and *Potentilla egedii.*

Compositional complexity increases landward. *Carex lyngbyaei* is still very common, but many other grasses, graminoids, and forbs are present. Some shrubs (mostly *Myrica gale*) also are present and seem to increase in density and distribution with distance inland.

The interlevee basins in the old marsh are presently dominated by herbaceous taxa; *C. lyngbyaei, Festuca rubra, Lathyrus palustris,* and *Cicuta douglasii* are the most common. Common taxa in shallow ponds are *Hipperus* spp*., Myriophyllum spicatum*, *Sparganium angustifolium*, and *Potamogeton* spp., but much of the pond is open water.

The vegetation of the foreshore levee is more complex. Shrubs (*Salix* spp., *Alnus crispa, Myrica gale*) are common. A few *Picea sitchensis* and *Populus balsamifera* trees are present. *Carex lyngbyaei* is still the most abundant herbaceous taxa, but several grasses (*Calamagrostis canadensis, Deschampsia beringensis, Poa eminens, Festuca rubra*) are locally abundant. *Epilobium* spp., *Equisetum* spp., and *Potentilla egedii* are the more common forbs.

Inland levees are dominated by herbaceous taxa, although *M. gale* forms small, dense stands in some areas. Vernal aspection is very prominent on the interior levees, and colorful wildflower displays are present in early summer. *Iris setosa*, *Lathyrus palustris*, and *Epilobium* spp. are common. The same graminoids as seen on the foreshore levee are present, and the fall aspect is a grassland.

Animals

Birds are the principal vertebrate animals using the Eyak River marsh. Species range in size from the trumpeter swan (*Cygnus buccinator*)[2] to the rufous hummingbird (*Selasphorus rufus*). Canada geese (*Branta canadensis*) nest in the old marsh and feed on the foliage and root systems of *Carex lyngbyaei* in the new marsh. Large areas of the sedge at the seaward edge of the new marsh often have an evenly mowed appearance from grazing by geese. Much of the grazing seems to have occurred at the time the sedge shoots were emerging from the substrate, because the outer portion of the leaves are all grazed to the same height. Geese tracks and droppings are common in the almost barren pans interspersed through the sedge stands. The geese may be feeding on *Puccinellia phyragnodes* or on algae. A great variety of other birds either migrate through the Copper River Delta or breed there. Mew and glaucous-wing gulls (*Larus canus* and *L. glaucescens*, respectively), Arctic

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[1] A complete list of plant taxa and scientific authority is given in appendix 1. Only the genus and species names are used in the text.

[2] Common and scientific names with authority for animals mentioned are given in appendix 2.

and Aleutian terns (*Sterna paradisaea* and *S. aleutica*), common snipe (*Gallinago gallinago*), and northern phalarope (*Lobipes lobatus*) all breed in the marshes. Bald eagles (*Halieetus leucacephalus*), marsh hawks (*Circus syaneus*), and short-eared owls (*Asio flammeus*) are the common avian predators.

Moose (*Alces alces*) were introduced to the Copper River Delta in the late 1950s and are the most important mammal. Beaver (*Castor canadensis*) are endemic and abundant. They have dammed many channels in the old marshes and created numerous impoundments. Brown bear (*Ursus arctos*), wolf (*Canis lupis*), coyote (*C. latrans*), and red fox (*Vulpes vulpes*) are the mammalian predators.

The narrow, steep-sided channels of the old marsh are used as rearing habitat by silver salmon fry (*Oncorhynchus kisutch*), which have spawned in the gravel beds of clearwater streams along the base of the surrounding mountains. The three spine stickleback (*Gasterosteus aculetus*) is common in the ponds of the old marsh and also may be found in flooded pans and small depressions in the new marsh.The boreal toad (*Bufo borealis*) is the only amphibian present. It can be quite abundant in the interlevee basin.

No live invertebrate consumers (crabs, burrowing worms, etc.) have been seen; however, empty shells of a small clam are common both on the substrate surface and buried in the mud. Mosquitos, gnats, biting flies, and other flying invertebrates are extremely abundant. Information on terrestrial, subterranean, and aquatic invertebrates is not available.

Previous Work

Trainer (1959) provides the earliest qualitative description of the preearthquake vegetation along the seaward edge of the wetlands. He recognized three vegetation types: sedge, mixed forb-low shrub, and alder-willow. In the sedge vegetation type, *Carex lyngbyaei, Ranunculus* sp., and *Triglochin* sp. were characteristic taxa. This vegetation was found "...adjacent to ponds and certain low sections of shoreline along the sloughs and gutters [sic] which are subject to frequent tidal inundation." The mixed forb-low shrub vegetation type was restricted to the "higher terrain which discontinuously parallels the watercourses." This higher terrain is the levee. Considerable driftwood was scattered throughout the mixed forb-low shrub vegetation type. The more important plants were the shrub *Myrica gale*, prostrate willow *Salix arctica*, and *Iris setosa*. Photographs accompanying the report show a vegetation dominated by graminoids with what appears to be the forb *Lomatogonium rotatum* prominent in one picture. The alder-willow vegetation type began about 5 kilometers inland and formed an ecotone with the spruce-hemlock forest of the lower mountain slopes. The understory of this shrub-dominated vegetation had "many of the plants typical of the two herbaceous [sedge and mixed forb-low shrub] habitats.

Even though these descriptions lack detail, they give a general impression of the vegetation present before the earthquake. They are the only descriptions available for the preearthquake marsh vegetation and, as such, are important because all the other information available is postearthquake.

The most important of the published postearthquake studies of the vegetation of the Copper River wetlands were made by Crow (1968, 1971, 1976). Three distinct physical habitats were recognized: channel banks, levees and other better drained uplands, and interlevee ponded basins. Within these, 13 wetland community types were described. Data on canopy coverage (Daubenmire 1959) and frequency data of taxa were collected to describe the subjectively determined community types of levee habitats, but similar data were not presented for the community types in channel and ponded basin habitats. Reactions (pH) by substrate textures and estimates of the preearthquake and current water regime and drainage conditions were used to reinforce the vegetation descriptions.

The major site features and dominant taxa of the 16 community types (C-T) according to Crow were:

Channel habitats:

Herbaceous vegetation—

Carex lyngbyaei C-T (no samples): steep lower, poorly drained channel banks; still subject to frequent tidal inundations; sparse, open stand.

Carex lyngbyaei-Eleocharis kamtschatica C-T (no samples): upper, less steep, slightly better drained channel banks; still flooded by tidal waters but less often; relatively dense stands of vegetation.

Levee habitats:

Herbaceous vegetation—

Hedysarum alpinum spp. *Americanum-Deschammpsia beringensis* C-T (10 samples): levees immediately adjacent to channels; silty, moderately well drained substrate; inundated by the highest tides before 1964.

Hedysarum alpinum spp. *americanum-Equisetum variegatum* C-T (1 sample): levees with sandy, better drained substrates; otherwise as above.

Low shrub vegetation—

Myrica gale var. *tomentosa-Poa eminens* C-T (5 samples): levees inland from channels with silty substrates; infrequently inundated by tidal water before 1964.

Mryica gale var. *tomentosa-Hordeum brachyantherum* C-T (1 stand): levees (as above) with sandy, better drained substrates.

Salix spp.-*Festuca rubra* C-T (5 samples): inland levees with silty, moderately well-drained substrates; no tidal flooding before 1964, but subject to river overflow.

Salix spp.-*Equisetum pratense* C-T (1 sample): levees with sandy, better drained substrates.

Salix spp.-*Calamagrostis canadensis* ssp. *canadensis*. C-T (1 sample): levee with poorly drained, somewhat acidic substrates.

Tall shrub vegetation—

Alnus sinuata-Arctagrostis arundinacea C-T (2 samples): most inland levees with sandy, well-drained, neutral-pH substrates, often on streambanks; inundated by river floodwater.

Alnus sinuata-Calamagrostis canadensis spp. *canadensis*. C-T (2 samples): levees with acidic, poorly drained substrates.

Coniferous woodland vegetation—

Picea sitchensis-Hylocomium splendens C-T (3 samples): well-drained, inland levees developed from gravelly glaciofluvial deposits.

Picea sitchensis-Strepttopus amplexicaulis; C-T (2 samples): silty, poorly drained, acidic substrates.

Ponded basin habitats:

Herbaceous vegetation—

Carex lyngbygei-Triglochin maritimun C-T (no samples): basin sites where the permanent water table was at or near the surface; occasionally flooded by tidal water in preearthquake conditions, still flooded by fresh water from runoff or precipitation.

Carex lyngbyaei-Latbyrus palustris ssp. *pilosus* C-T (no samples): slight rises in the basin habitat where the water table was relatively deep beneath the surface.

Carex lyngbyaei, Cicuta mackenzieana C-T (no samples): basin sites with a more or less permanent surface water table.

Crow's (1968, 1971, 1976) community types are valuable because they are almost the only available information on the immediate postearthquake vegetation of the western Copper River Delta wetlands. The classification of the levee habitats seems detailed and stresses environmental differences as controlling influences; however, it has some limitations. It is based on the Daubenmire (1959) method in which stands of vegetation that appear to the observer to be similar in structure and composition and are spatially repeated are subjectively selected and mentally abstracted into classification units. Stand attributes are sampled only to provide descriptive criterias and not to develop the classification units. Vegetation (and site) attributes from included stands are not generalized to provide the descriptive attributes of the classification units.

Between 1975 and 1977, the College of Forestry, University of Minnesota, produced a rectified, 1:15840-scale cover-type map of much of the wetland area of the western Copper River Delta (Potyondy and others 1975; Scheierl and Meyer 1976, 1977). The work basically was direct photogrammetric interpretation in the early stages, but ground-truth data were collected subsequently. The photographs were true-color Ektachrome taken between 1974 and 1977.[3]

The vegetation-site mapping unit symbols were:

S: sedge (interlevee basins)

S_i: invading sedge (earthquake-uplifted tidal flats, river sandbars, and beaches)

G: grass-forb (levees)

E: dunegrass (stabilized sand dunes on offshore barrier islands)

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[3] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

E_i: invading dunegrass (active dunes, early stage of sand dune succession)

S_b: sedge-bog transition (the floating mat stage of pond succession)

M_t: muskeg meadow (the anchored mat stage of pond succession)

M: muskeg (upland sphagnum bog)

Woody cover types

W: willow-sweetgale (levees: willow could not be distinguished from sweetgale in the photographs)

A: alder (levees, outwash plains, streambanks, river terraces)

P: cottonwood (stabilized sand dunes, outwash plains, river terraces)

S_p Spruce (gravelly outwash plains, rocky uplands, rock islands in marshes)

Substrate cover types

B_s: bare silt surfaces

B_g: bare gravel surfaces

D: drifting sand dunes, ocean beaches

T: undifferentiated tide flats

Aquatic cover types

No symbols; ponds were dark colored on maps, flowing water uncolored.

Additional subscripts and superscripts were used to indicate shrub and tree crown coverage in three percentage classes (10-40, 41-709,and 71-100) and shrub height in two classes (> 1.5 meters, < 1.5 meters). Tree heights were not estimated. Symbols were combined, where needed, to identify mapping units.

The cover-type maps included much more of the Copper River Delta than the areas examined by Trainer and Crow, and several additional types of vegetation are listed. These represent either the early stages of postearthquake succession, which were visible on the photographs, advanced stages of wetland succession taking place on the most inland of the tidal marshes, or vegetation on habitats not present in the outer marshes.

When mapping units are progressively developed as mapping proceeds, new units may be the result of true differences or additions due to geographic locations, to intergradation from site continua, or from plant succession (time continua). New mapping units also may be caused by better photogrammetric interpretation. As the interpreter's experience increases, a better understanding of what is visible in the photographs occurs. This leads to a tendency to continually subdivide already established mapping units and a consequent proliferation of mapping units. Unless very careful account is kept, a cover type likely will be given a different symbol or title in a new location. All these problems are present on the cover-type maps prepared for the Copper River Delta; nevertheless, the maps give a useful account of the wetland vegetation. The sedge, grass-forb, willow-sweetgale, and alder cover types are comparable to the vegetation units of Trainer and Crow. Because they are two-dimensionally portrayed, the maps provide an estimate of the relative proportion of the vegetation types and of their areal extent and juxtaposition on the landscape 10 years after the 1964 uplift.

Batten and others (1978) provide the most recent evaluation of tidal marsh vegetation on the Copper River Delta and elsewhere along the south-central gulf coast of Alaska. For the Copper River Delta, samples were limited to the immediate boundary between the preearthquake marsh and the new marsh. Taxon crown coverage was estimated with a 10-percent interval scale. Batten and his coauthors have an excellent background in taxonomy, but because sample plots were arranged along a transect line located at right angles to the foreshore levee and may cross distinct environmental gradients (elevation changes, substrate and drainage differences, salinity gradients, and so forth), it is difficult to develop vegetation types from the data. Trends in abundance-dominance of taxa over a short distance were illustrated, however.

Study Area

This study was carried out on the marshes to the west of the mouth of the Eyak River (fig. 2). All the terrain features previously described for the western Copper River Delta wetlands were present there. In addition, the area had the greatest seaward extension of all the postearthquake tidal marshes. For efficiency in travel and in field sampling, the actual area studied was limited to the marshland between the Eyak River and Center Slough, the first major distributory channel to the west: an area of about 165 hectares.

Methods

Field Methods

Marsh elevation—Existing 1:63,360-scale topographic maps were based on preearthquake aerial photographs, but the mapping scale was too coarse to allow elevations of the study site to be determined. To determine those elevations, a level line was surveyed from a State Highway Department benchmark 9.7 kilometers north of the mouth of the Eyak River beside the Copper River highway. A surveying compass and a rod precise to 0.03 meter were used. The line was surveyed twice, over different routes, but was not closed. Distance was not measured. A semipermanent benchmark was established on the foreshore levee at the mouth of the Eyak River.

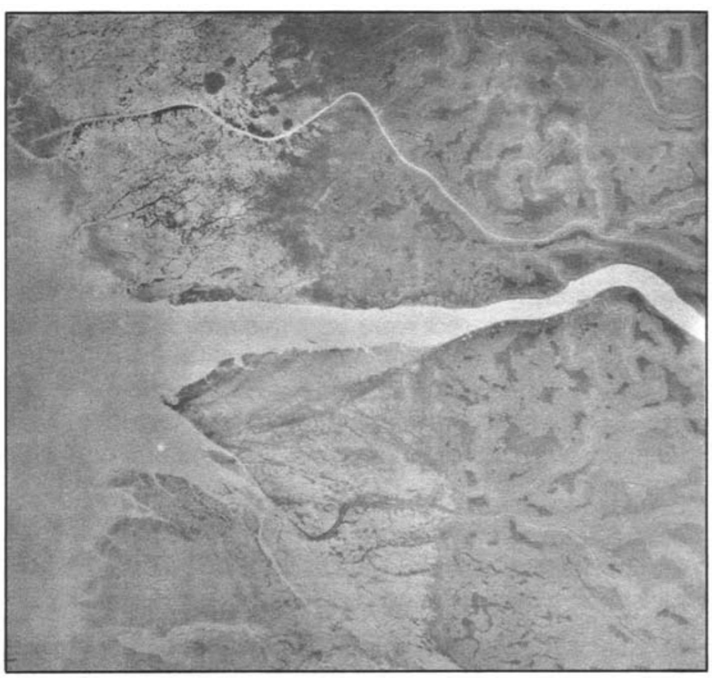

Figure 2—The Eyak Marsh study area in 1974.

Six additional level lines were surveyed on the major terrain and habitats within the study area itself. In the old marsh, these were foreshore levee, interior channel levee, and marsh basin. In the new marsh, lines were surveyed on the river levee, the marsh basin, and the channel levee of Center Slough. Elevation was determined at 30-meter intervals along transects paralleling the long axis of all levees and on a single seaward-oriented transect in the new marsh basin. The transect in the old marsh basin was subdivided into three segments but was considered as a single transect for subsequent sampling.

Tidal regime-Because the tide at the Eyak River Marsh is not gauged and the closest established tide gauge is at Cordova on Prince William Sound, about 22 kilometers to the northwest, Stock's (1980) tide model was used to determine the height and duration of the tide. Tide height to the nearest 0.1 meter and time of high and low tides were obtained from the published tide tables for Cordova Station (U.S. Department of Commerce 1979a). Height and time were corrected for the Eyak River entrance. Time was converted to a decimal fraction (nearest 0.001 hour) of the total hours in a year. Elevations were those obtained from the leveling survey. The program was modified to include an estimate of photoperiod, calculated as the daily sunrise to sunset interval minus 30 minutes at sunrise and plus 30 minutes at sunset. The local mean sunrise-sunset data for 60° N. latitude (U.S. Department of Commerce 1979b) was extrapolated to 60° 48' N., the latitude of the Eyak River entrance. Because the random variables of atmospheric pressure, direction and force of the wind, precipitation, and river runoff levels were not included, the inundation period determined from the model is only an index for relative comparison.

Physical habitat—The extent and relative proportion of the various physical habitats on the Eyak River Study site were determined with a dot-grid overlay (64 dots/in^2) on the 1974, 1:15840-scale aerial photograph.

Vegetation sampling—Data on taxa composition, canopy coverage, and distribution were collected for (1) describing the Eyak River marsh, (2) classifying phytosociologically, and (3) comparing succession in the new and old marshes. The sampling sites for data collection were located by restricted random selection of 25 percent of the survey stations on the transects where elevation had been determined.

There were two restrictions on the randomizing of sample locations. First, because there was much greater complexity in taxa composition in the first 300 meters of new marsh seaward of the foreshore levee, at least 40 percent of the selected samples in each leveling transect were from this area. Second, in the old marsh, selected sample sites were separated by at least 60 meters (two elevation stations). This allowed the total elevational gradient from foreshore levee to seaward edge of the vegetation in the new marsh to be sampled, and it distributed the sample sites throughout the total length of the old marsh transects.

Each selected station located the start of a 20-meter-long vegetation sampling transect. Sampling transects were run at 90° to the level transect (that is, along the contour rather than across it). Each transect had 20 0.1-centare quadrats located systematically at 1.0-meter intervals.

Number and area of quadrats was determined from preliminary tests in the floristically more complex old marsh and may have oversampled the floristically simple new marsh.

Canopy coverage (Daubemire 1959) was used to sample the vegetation. Canopy coverage of each plant taxon, of bare substrate, and of standing water was estimated with eight classes in place of the original six classes.

Class	Range	Midpoint	Description
	- - - *Percent* - - -		
1	0	0.1	Present
2	1	.5	Trace
3	1-5	3.0	Rare
4	6-25	15.0	Minor
5	26-50	38.0	Common
6	51-75	63.0	Abundant
7	76-95	85.0	Major
8	95-100	98.0	Complete

Class 1 has no coverage range and was used for taxa not present on any quadrat, but that were present within 2 meters of either side of the transect line. This convention allowed all taxa in the immediate location to be recorded and evaluated.

The 20 individual class estimates of canopy coverage were converted to the midpoint values and averaged to provide a single measure of the canopy coverage of an individual taxon at each sample site. To minimize ties, average estimates were rounded to the nearest 0.1 percent. Because the estimates were made in classes, no statistical measure of variation, except the range in classes, was available for within-site samples. Statistical variance can be calculated when taxon values from a number of stands are averaged. Although canopy coverage was estimated and is presented as a percentage, the values also represent an average proportion of a 1000-square-centimeter^2 quadrat covered by a given taxon and could be expressed in square centimeters. The canopy coverage method provides an automatic estimate of taxa frequency or the number of quadrats on which a taxon is recorded as a percentage of the total number of quadrats used. Class 1 taxa have coverage values but no frequency values. A 4- by 20-meter area bisected by the transect was considered an unmarked stand macroplot and allowed the computation of constancy values for each taxon. Constancy is the percentage of stands of a specific area on which a taxon occurs. Class 1 taxa have constancy values.

Substrata description—A coring tool (Brown and Thilenius 1977) was used to extract two 6.5- by 30-centimeter cylindrical cores from each site. Cores were examined in the field for thickness and nature of the organic layer and texture and structure of the inorganic material. Depth of the water table below the uppermost surface of the substrate was measured to the nearest centimeter about 1 hour after the core was extracted.

Temperature-corrected salinity and conductivity of the soil water were measured in the field with a Y.S.I. Model 33 salinity meter. Soil water reaction was determined in the laboratory from 200-milliliter samples collected in the field. A VWR Model 55 Mini-pH meter was used. Temperature range was 19 to 20 °C.

Analytical Methods

Numerical classification-Agglomerative, polythetic, numerical cluster analysis was used to classify the stands into vegetation types. Programs SlMlD and CLUST (Volland and Connally 1978) were used to develop the classification. SlMlD uses the Sorensen coefficient to calculate the initial matrix of similarity. CLUST performs a hierarchical cluster analysis of the similarity matrix produced by SIMID. The average linking sorting strategy was selected. Percentage of canopy coverage was the numerical value.

Before numerical analysis was done, the vascular plant taxa by stand data matrix collected in 1983 was modified as follows:

1. Vascular plant taxa were grouped into three physiognomic categories: woody taxa (shrubs and trees), graminoids (sedges and grasses), and forbs (all other vascular plants), and the total canopy coverage provided by each category was calculated.
2. Vascular plant taxa in each physiognomic category with an average within-stand canopy coverage of less than 1 percent were combined into the category "other."

Four additional attributes that could be evaluated by the canopy coverage method also were included in the data matrix: attached dead and litter, total cryptogam (mosses, lichens, algae) coverage, bare substrate, and standing surface water. The final data matrix used for classification was 63 stands by 27 attributes.

The results of SIMID-CLUST analysis commonly are presented in a two-dimensional dendrogram. One axis of the dendrogram separates the stands and has no scale. The other axis is scaled in units of similarity. Sample stands are arranged linearly along the stand axes by their overall similarity. Clusters of stands related to other clusters of stands only at low levels of similarity were selected initially by visual inspection of the dendrogram. These clusters formed the preliminary array of classification units.

Discriminant analysis (SPSS program DISCRIMINANT; Klecka 1975) was used to test the proportion of stands misclassified by numerical cluster analysis. Analyses were made from the full model (number of discriminant functions = number of groups - 1; maximum significant F to enter attribute = 0.05) and on various reduced models (lesser number of discriminant functions and of attributes). The influence of moving misclassified stands to the highest probability group on the subsequent classification also was investigated.

Classification units were described by calculating the mean and standard error of each included attribute. To aid comparisons, plant attributes were stratified by physiognomic group and ranked in descending order of the mean attribute value within a stratum. The plant taxon with the greatest canopy coverage in each strata was used to name the classification unit. For clarity, other characteristic taxa occasionally were included in the name, and the predominant habitat where the included stands were located also was used.

After the final number of classification units had been determined and the proper order of included stands established, another numerical cluster analysis was carried out. For this, the similarity matrix was based on the mean values of the attributes of the stands included within each classification unit. This second classification allowed the overall similarities of the vegetation types to be established.

Table 2—Areal extent of wetland habitats on the Eyak River Marsh, 1974

Habitat	Area	
	Hectares	*Percent*
New marsh:	105.2	100
River levee	2.3	2
Slough levee	3.3	3
Tidal flats—	99.6	95
High marsh	19.6	19
Low marsh	80.0	76
Old marsh:	60.2	100
Levees and channel banks—	16.8	27
Foreshore	2.5	4
Interior	8.6	14
Basin—	43.4	73
Marsh	36.6	62
Ponds	6.8	11
Eyak River Marsh:	165.4	100
Old marsh	60.2	36
New marsh	105.2	64

Successional changes in the vegetation of the Eyak River wetlands were examined in two ways: by group and by individual taxon. In the first, data on composition and canopy coverage collected in 1979 from the 63 stands were arranged in the order of stands within groups as determined by the 1983 cluster analysis. The model attributes of the nine groups in 1979 were determined and a cluster analysis was performed to obtain the similarities of the nine 1983 groups as they were in 1979. In the second, the statistical significance of the 1983-79 differences in canopy coverage of the model attributes of the 10 characteristic taxa and of logical summations of taxa was determined. Because of unequal variances. and sample size, the nonparametric Mann-Whitney-U test was used in place of the t-test (Siegel 1956) to determine the statistical significance of differences in attribute values.

Results Wetland

Habitats

The areal extent and relative proportion of the wetland habitats on the Eyak River Marsh are given in table 2. The aerial photograph from which the estimates were made (fig. 2) was taken in 1974, and the habitats and areas are those present 10 years after the uplift. No detectable changes in type or area of the habitats appeared to have occurred by the 1979-83 period. Unfortunately, more recent aerial photographs of similar scale, color, and quality to those of 1974 are not available to make a more quantitative comparison.

Wetland Vegetation

Floristics—One hundred and eight vascular plant taxa were present on the 63 sample stands. Graminoids were much more common than forbs or shrubs. The most ubiquitous and abundant plant was the sedge *Carex lyngbyaei*. It occurred in all stands on both new and old marsh and usually had the greatest canopy coverage of any taxon in the stand. It was very abundant on new marsh, especially in seaward locations where it occurred as a virtual monoculture.

The species richness on the new marsh increased landward; that is, as the potential frequency of tidal inundation decreased. The more landward portion of the new marsh is a transition zone between the two major habitats. Because of this, many taxa were present in both major habitats, but except for *C. lyngbyaei* and the prostrate forb, *Potentilla egedii*, the canopy coverage of individual herbaceous taxa was greater in the old marsh.

The shrub *Myrica gale* was the second characteristic taxon of the marshes. It was most abundant in the old marsh where it was confined almost entirely to levee and channel bank habitats. In the new marsh, it was more prevalent in the least tidal locations, but it could persist on organic mounds in locations where tidal inundation was frequent and of relatively long duration. *Myrica gale* fixes atmospheric nitrogen through a possibly symbiotic relation with the actinomycete *Frankia* sp., and the roots are heavily modulated even in tidal habitats. It is better able to grow on substrates with more or less permanent high water tables, and consequent poor aeration, than the other major shrub taxa, *Alnus crispa* and *Salix* spp., also present in the Eyak Marsh. Of the remaining taxa, the grasses *Calamagrostis canadensis, Festuca rubra*, and *Deschampsia beringensis* and the forbs *Cicuta douglasii, Equisetum arvense,* and *Potentilla palustris* were the most abundant and widely distributed, especially in old marsh habitats.

Phytosociological Units

Numerical classification—Classification was based on a 63-stand by 27-attribute matrix. The most recent data (1983) were used. Nine groups of stands were initially defined (fig. 3). Discriminate analyses indicated 59 of 63 of the stands (94 percent) were correctly classified by numerical analysis. The data sets for the four misclassified stands were shifted to the indicated correct group and the discriminate analysis rerun. Correct classification increased to 97 percent (61 of 63 stands). One further iteration gave 100-percent-correct classification but reduced one group to a single stand. In addition to the development of nine groups, numerical classification arranged the groups into two sections corresponding to the new and old marsh habitats.

The abbreviation C-T (for community type) is used for the groups of stands defined by the classification procedures. A community type is an abstract phytosociological classification unit—a conceptual entity with modal attributes derived from the real attributes of the stands it was developed from. Because it is defined by unweighted, shared, multiple attributes, it is polythetic in nature (Sokal and Sneath 1963). Consequently a stand that “belongs” to a given community type need not have all the attributes used to describe the classification unit, and no single attribute is either essential or sufficient for inclusion. The term is an abstraction.

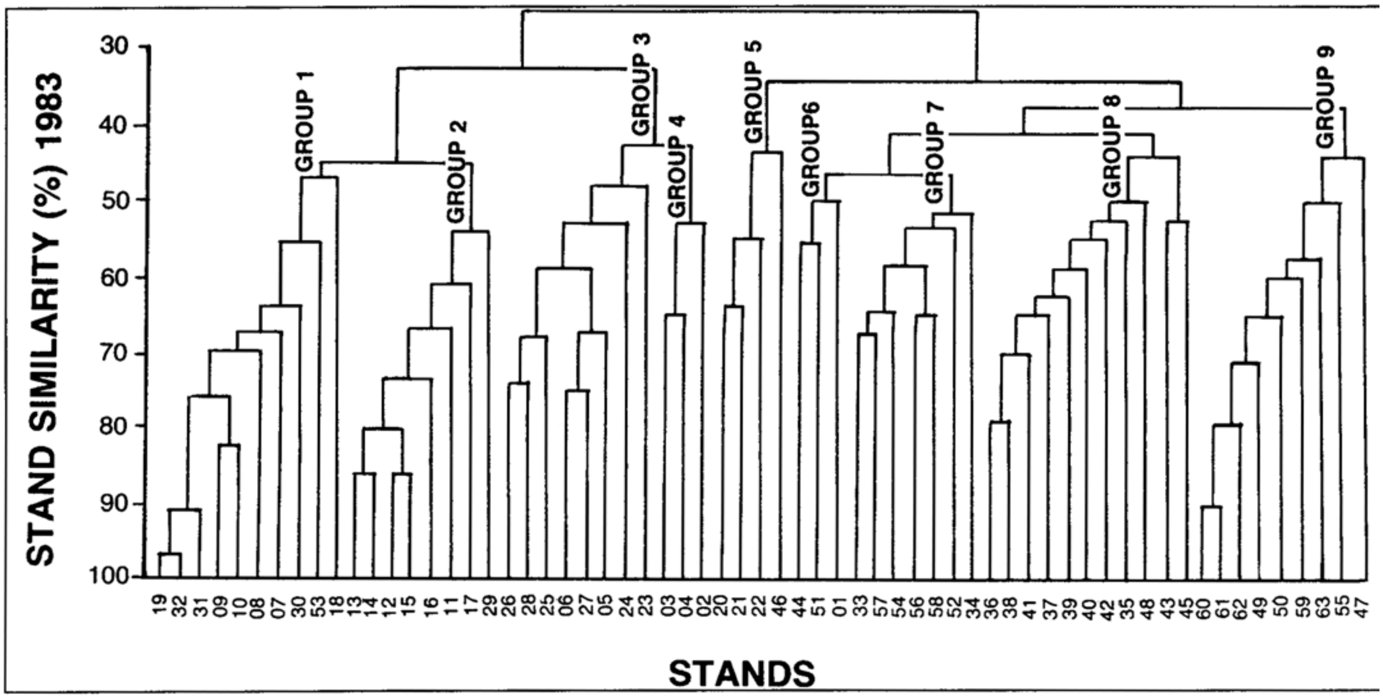

Figure 3—Dendrogram of the initial 63stands by 27-attribute cluster analysis of the 1983 data.

Although a community type is polythetically defined (Clifford and Stephenson 1979), it has been named for the plant taxa in each stratum with the greatest average attribute values calculated from the values of the included stands. Here, these are called characteristic taxa. “Characteristic” is used in preference to “dominant” because the former does not imply the presence of any form of control. For brevity, only the genus is used to designate community types. An additional designator based on the habitat where the stands representative of the community type occurred also is used. Where distinct vegetation strata are present, the genus names are separated by a virgule (/).

The nine community types present in 1983 were:

New marsh (tidal habitats):

Carex C-T (low marsh)

Carex C-T (high marsh)

Carex/Potentilla C-T (low levee)

Myrica/Carex-Potentilla C-T (high levee)

Old marsh (nontidal habitats):

Alnus/Myrica-Salix/Carex C-T (foreshore levee)

Myrica/Carex-Calamagrostis (foreshore levee)

Carex/Equisetum-Lathyrus C-T (interior levee)

Carex/Lathyrus C-T (moderately hydric interlevee basin)

Carex-Cicuta/C-T (hydric interlevee basin)

Narrative descriptions of the important modal vegetation features of the community types are given below. Detailed information on taxa composition and canopy coverage is in the appendix (tables 5 through 15), and the appearance of the vegetation of selected examples of each community type is illustrated in figures 4 (1983) and 5 (1979).

New Marsh Community Types on Tidal Habitats

C-TI *Carex* C-T on low new marsh habitats (13 stands)—

Structure—This is a moderately dense, single stratum, graminoid meadow composed almost entirely of one species of sedge from 30 to 60 centimeters in height. Total canopy coverage of vascular vegetation is 69.9 percent. No shrubs are present, and a low herb stratum also is absent. Uprooted and transported seaweed and algae cover one-fourth of the ground surface. Total live vegetation cover is 74.7 percent.

Composition—Canopy coverage of *Carex lyngbyaei* is 63.3 ± 9.5 percent. *Potentilla egedii*, a prostrate stoloniferous forb, is the only other species to exceed 1 percent canopy coverage. A few other herbaceous taxa (*Deschampsia beringensi, Puccinellia phrygnodes, Triglochin palustre, Juncus arcticus*, and *Cicuta douglasii*) are sporadically distributed in the ground stratum at very low levels of canopy coverage. Canopy coverage of attached dead plant material is 24.9 percent.

Habitat—Stands representative of the community type are found in the most seaward portion of the new marsh. Mean elevation is 2.4 ± 0.68 meters above mean sea level. The comparative tidal exposure index for the growing season at this elevation is 78.6 percent (2358.4 hectares) with 162 floodings per year. True litter (unattached dead plant material) is removed by tidal action. Unvegetated silt and fine sand cover 72.1 ± 9.8 percent of the ground surface beneath the vegetation. This will vary greatly over short periods because the current ground surface cover is dependent on the duration of the tide and the suspended sediment load of the immediately preceding flooding tide. The substrate is interbedded layers of inorganic sediments and the dead, but still attached, leaves and seedheads of sedge buried by the tide-deposited sediments. A standing water table is at or near the surface. Sapropel made up of anaerobic organic debris is present at depths of 30 centimeters or more.

C-T2: Carex C-T on high new marsh habitats (8 stands)—

Structure—This is a densely vegetated graminoid meadow with the tallest stratum almost entirely of one species of sedge 30 to 50 centimeters tall. A few scattered individual shrubs are present. A poorly developed low herb stratum is present as is a dense ground stratum of attached dead sedge leaves with some litter and cryptogams (mosses, liverworts).

Composition—*Carex lyngbyaei* has a canopy coverage of 80.9 ± 5.0 percent. *Myrica gale* has less than 1 percent canopy coverage. The grasses *Calamagrostis canadensis* and *Festuca rubra* occur but neither exceeds 1 percent canopy coverage. *Potentilla egedii* is the most common forb and the only herb other than *Carex lyngbyaei* to exceed 1 percent canopy coverage. *Salix barclayi* and *Salix commutata* and the prostrate willow *Salix arctica* are the other shrubs, but they are uncommon and widely distributed.

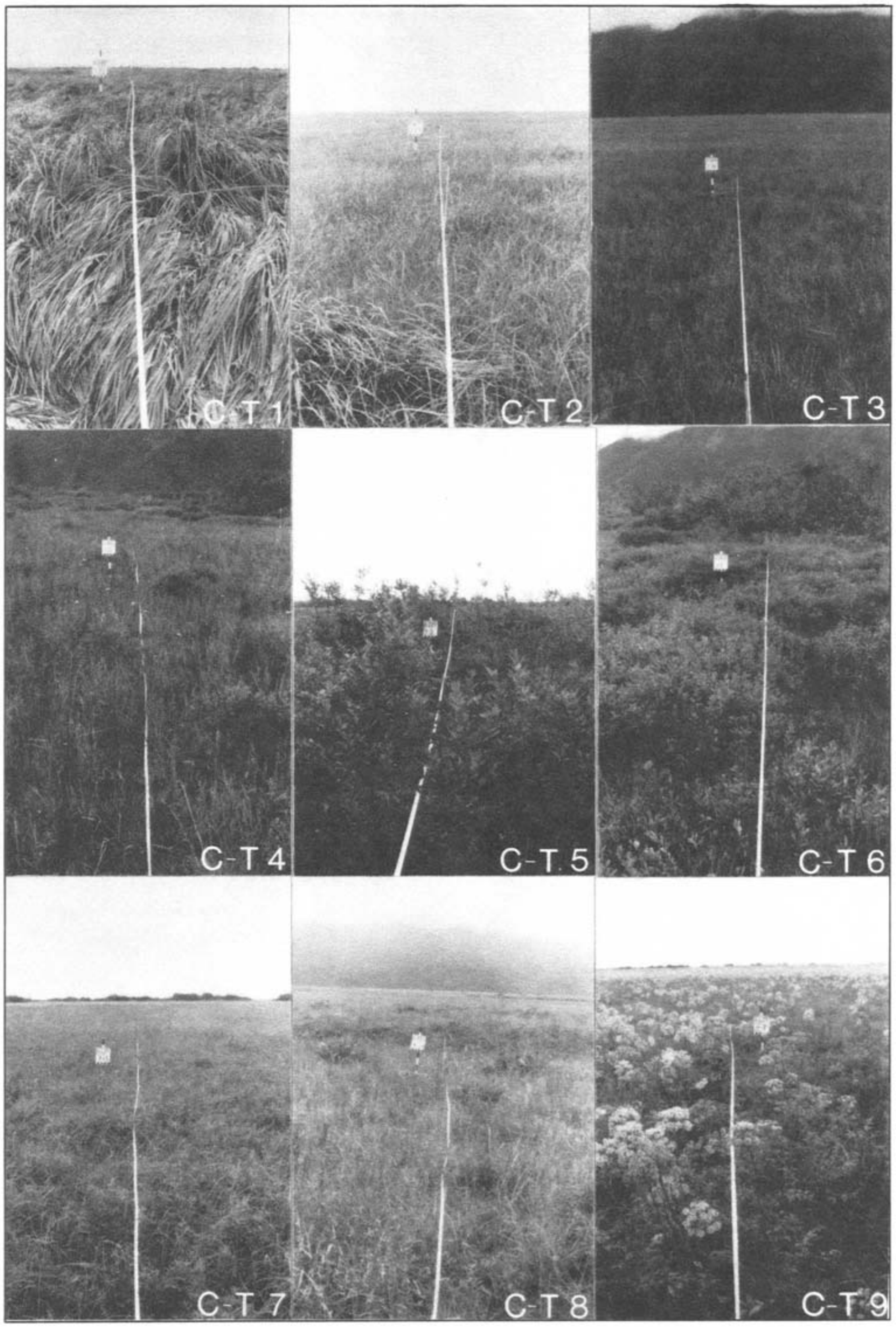

Figure 4—Eyak marshland community types in 1983. C-TI, *Carex* low marsh; C-T2, *Carex* high marsh; C-T3, *Carex-Potentilla* low levee; C-T4, *Myrica-Carex* high levee; C-T5, *Alnus/Myrica-Salix* high levee; C-T6, *Myrica/Carex-Calamagrostis* foreshore levee; C-T7, *Carex-Lathyrus* mesic basin; C-T8, *Carex-Equisetum-Lathyrus* interior levee; C-T9, *Cicuta/Carex-Festuca* hydric basin.

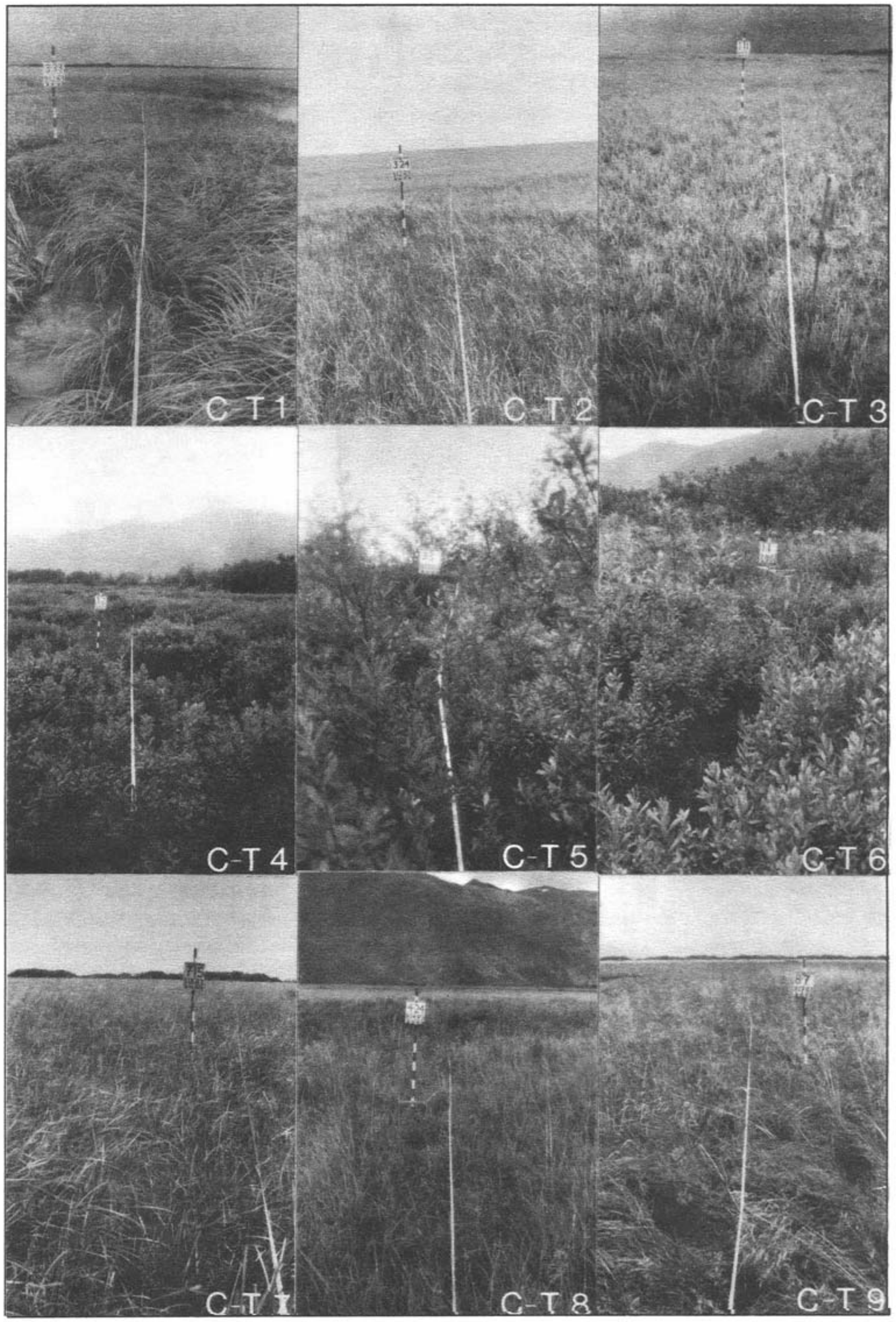

Figure 5—Eyak marshland community types in 1979. C-TI, *Carex* low marsh; C-T2, *Carex* high marsh; C-T3, *Carex-Potentilla* low levee; C-T4, *Myrica-Carex* high levee; C-T5, *Alnus/Myrica-Salix* high levee; C-T6, *Myrica/Carex-Calamagrostis* foreshore levee; C-T7, *Carex-Lathyrus* mesic basin; C-T8, *Carex-Equisetum-Lathyrus* interior levee; C-T9, *Cicuta/Carex-Festuca* hydric basin.

***Habitat*—**This community type is found in the new marsh at more inland, higher elevation (3.4 ± 0.3 meters) nonlevee sites. Tidal exposure index is 97.1 (2913 hectares) with 46 floodings. Bare silt covered only a relatively small portion of the ground surface under the vegetation. The surface substrate has a well-defined organic layer up to 10 centimeters thick overlying densely packed glacial silt. A standing water table is present at a depth of -5 centimeters or less. Sapropel is absent.

C-T3: *Carex/Potentilla* C-T on low new marsh levee habitats (7 stands)—

***Structure*—**This two-strata graminoid meadow has a moderately dense stratum of sedge and grasses above a herb stratum dominated by a single species of a prostrate-to-partly-erect stoloniferous forb. The graminoid stratum is 20 to 40 centimeters in height; the forb stratum rarely exceeds 10 centimeters in height. Small shrubs are present at low constancy in the upper stratum, and a prostrate shrub occurs in the herb strata. Total canopy coverage of live vascular plants is 91.5 percent. Attached dead matter and litter covers 60.5 to 8.3 percent of the surface.

***Composition*—**The sedge *Carex lyngbyaei* is the most important graminoid in the upper stratum, but the grasses *Festuca rubra* and *Deschampsia beringensis* are also abundant locally. The visual aspect of this community type changes from sedge dominance in spring to grass dominance in fall. Grasses become more visible in the later part of the growing season owing to the development of flowering culms. Nevertheless, *Carex lyngbyaei* is by far the most abundant taxon at all times of the year (54.6 ± 10.6 percent canopy coverage). Compared to the other two new marshland sedge community types, total forb canopy coverage is much greater in this new marshland community type mostly because of the canopy coverage by *Potentilla egedii* (22.1 ± 3.7 percent). The bright yellow flowers of *Potentilla egedii* bloom throughout the growing season and are quite conspicuous. *Eguisetum arvense* and *Juncus arcticus* are the more important of the less abundant forbs. The latter may grow in distinct, monospecific stands at the least tidal locations. The cryptogamic stratum is not well developed.

***Habitat*—**New marshland levees subject to relatively frequent tidal flooding support this community type. These levees occur next to the seaward portion of the water courses of glacial rivers, the major distributary channels, and the larger drainage channels originating in the interlevee basin habitat of the old marsh. The community type is not yet present on the levees of minor tidal channels that drain the new marsh. Mean elevation above sea level is 3.27 ± 0.36 meters. The comparative flooding index for the community type is 96.0 percent (2879.0 hectares) with 56 floodings.

A layer of recently deposited sediments covers over one-quarter of the ground surface. Sands are more common than silts, both on the surface and in the substrate. The coarse sediments promote drainage in the upper 5 to 10 centimeters of the substrate, and most of the fine roots of all the plants are present here. The surface of the levee is slightly elevated relative to the surface of the immediately adjacent interlevee basin on one side and most of the time is several meters above the level of water in the channel on the other side. The presence of the coarse sediments improves the possibility of lateral drainage of subsurface water, and the surface substrate is relatively well drained by tidal wetland standards. The standing water table is usually at depths of -20 centimeters or more except immediately after tidal flooding or intense rainfall.

C-T4: *Myrica/Carex* C-T on high new marsh levee habitats (1 stand)—

Structure—This community type is a multistrata shrubland characterized by very dense stands of Myrica gale in the shrub stratum and by a mixture of sedge, grasses, and forbs in the herbaceous strata. A thick, complete ground cover of attached dead plant material and litter is present. Total canopy coverage of vascular vegetation is 137.5 percent.

Composition—*Myrica gale* forms an almost complete (87.2 percent) shrub cover 60 to 90 centimeters tall. Individual *Salix barclayi* and *S. commutata* up to 1.5 meters tall are scattered through the dense stand of *M. gale*. Some *S. arctica* are present in the herb layer, and the total shrub cover approaches 100 percent. The understory stratum is relatively open and not particularly species rich. *Carex lyngbyaei* is still the most common graminoid; but *Festuca rubra, Calamagrostis candensis, Agrostis exerata,* and *Deschampsia beringensis* are relatively abundant. *Potentilla egedii* is the most abundant forb. It grew taller and had larger leaves in this community type than elsewhere. *Juncus arcticus, Galium trifidum, Cicuta douglasii,* and *Iris setosa* are present but not abundant. Cryptogams are relatively uncommon in the ground stratum.

Habitat—The community type occurs only on the high-elevation portion of levees in the new marshland (4.0 meters above mean sea level) and is found immediately below the foreshore levee. At this elevation, the comparative exposure index is 99.9 percent (2996.3 hectares) with only four inundations during the May-September growing season. Flooding water is not even minimally brackish. Because of the geographic location, laterally draining fresh water from the old marsh naturally irrigates the site, and the water table is usually within 10 to 15 centimeters of the substrate surface. A layer of partially decomposed organic material is present under the litter layer. The leaves of Myrica gale are especially evident in this layer. Beneath is a 2- to 5-centimeter-thick layer of light-colored, crumb-structure inorganic material, below which is tightly compacted glacial silt. In situ soil water reaction is very acidic; pH 4.5 values and below were common.

Old Marsh Community Types On Nontidal Habitats

C-T5: *Alnus/Myrica-Salix/Equisetum* C-T on old marsh foreshore levee (4- stands)—

Structure—This community type is a shrubland with both a tall-shrub and low-shrub stratum. The tall-shrub stratum is 3.0 to 4.5 meters tall and moderately dense. The shrubs in the low-shrub stratum rarely exceed 1.0 meter.

A moderately species-rich herbaceous stratum is present. Forbs are the predominant taxa, but several graminoid taxa also are present in moderate abundance. The ground surface has an almost complete cover of litter and attached dead plant parts 10 to 15 centimeters thick and a moderate cover of cryptogamic taxa. Total coverage of the vegetation 172.5 percent. The shrub strata produces 92.6 percent of this coverage.

Composition—*Alnus crispa* var. *sinuta* is the major shrub in the tall-shrub stratum. A few *Salix commutata* and *S. sitchensis* also are present. These two shrubs are sympatric in many other locations in the Copper River Delta wetlands. The low-shrub strata is an intermixed stand of *Myrica gale* and *S. barclayi* in approximately a 2-to-1 ratio, based on canopy coverage. Small *A. crispa* are present, but uncommon, in the low shrub stratum. A few *Picea stichensis* and *Populus trichocarpa* occur. *Equisetum arvense* is the most abundant single taxon in the herbaceous stratum, but *Carex lyngbyaei* and *Calamagrostis canadensis* also are important herbaceous taxa. The cryptogamic stratum is composed of mosses, liverworts, and *Sphagnum* spp.

***Habitat*—**This community type occurs on the foreshore levee at the seaward edge of the old marshland. The average elevation is 4.5 ± 0.4 meters. Because the extreme high spring tide level is 4.2 meters, the foreshore levee is rarely inundated. The combination of extreme spring tides, elevated sea levels due to low atmospheric pressure (storm surge), strong onshore winds, and high river runoff might still flood the foreshore levee. No evidence of recent tidal inundation is present (particularly garbage, net floats, and other flotsam from inshore fishery operations). The presence of large driftwood logs (30 to 50 centimeters in diameter, 5 to 10 meters long) now incorporated into the crytogamic stratum are evidence of preearthquake tide levels well above the surface of the foreshore levee. The upper 20 to 30 centimeters of the inorganic substrate is relatively well drained and tends to have loamy to sandy texture and subangular blocky structure. Standing water may occur below 30 centimeters. In locations not directly occupied by living vegetation, there is a relatively thick litter layer (5 to 10 centimeters) composed mainly of shed shrub leaves in all stages of decomposition.

C-T6: *Myrica/Carex/Calamagrostis* C-T on foreshore levee habitats (3 stands)—

***Structure*—**The vegetation of this community type is a multistrata shrubland with the shrub stratum less than 1 meter tall. Graminoids are the predominant taxa in the herbaceous layer. Forb taxa are numerous but did not contribute greatly to the total canopy coverage of live vegetation of 144.1 percent. The ground stratum has a complete cover of litter, attached dead plant material, and crytogamic taxa.

Composition*—Myrica gale* and *Salix barclayi* are the major contributors in the shrub stratum. *Myrica Gale* is by far the most abundant shrub. *Alnus crispa* is present but uncommon. *Carex lyngbyaei* and *Calamagarostis canadensis* contribute almost equally to the herb stratum; *Festuca rubra* is the third most important graminoid. The more important forbs are *Equisetum arvense, Epilobium hornemannii, Lathyrus palustris*, and *Galium trifidum*.

***Habitat*—**This community type occurs on the foreshore levee in the same general habitat as the *Alnus/Myrica-Salix/Equisetum* C-T, and the description of the habitat of the latter applies here. The major difference in the vegetation is the absence of the tall-shrub stratum of *A. crispa*, which occurs but is not common in this community type. In the Copper River Delta wetlands, *A. crispa* is most abundant on coarse-textured (gravel and sand), well-aerated substrates in locations that have fluctuating near-surface water tables in the growing season. *Myrica gale* grows best on more-or-less permanently flooded sites with glacial silt substrates that are poorly aerated. Thus, a difference in substrata texture or drainage characteristics might be the cause of the absence of *A. crispa*. No such differences are readily apparent, however, at the locations where this community type occurs and the *Myrica/Carex/Calamagrostis* C-T may represent an early seral stage of the *Alnus/Myrica-Salix/Equisetum* C-T. The two community types currently are phytosociologically distinct.

C-T7: *Carex/Equisetum-Lathyrus* C-T on interior levee habitats (12 stands)—

Structure—his community type is a species-rich, mixed herbaceous meadow. Total live vegetation coverage is 162.4 percent. Forbs are the predominant plants, especially during the first half of the growing season when there is an exceptional display of showy wildflowers. The fall aspect is a grassland. Several shrub taxa are present at low density. Most grow along the break in slope between the channel bank and the levee surface. Sedge is more prevalent on the inner side of the levee where it gradually intergrades into the interlevee basin habitat. The cryptogamic and litter strata completely cover the ground surface in a layer more than 20 centimeters deep.

Composition—The most abundant species is *Carex lyngbyaei* Major grasses are *Festuca rubra, Deschampsia beringensis*, and *Calamagrostis canadensis*. *Agrostis exerata* and *Poa eminens* and several *Carex* spp. are minor graminoid components. *Equisetum arvense* is the most abundant forb, and *Lathyrus palustris* also is abundant. Other important forbs are *Potentilla egedii, lris setosa, Galium trifidum*, *Epilobium hornemannii*, and *E. angustifoluim*. The fern *Athyrium filix-femina* attains its greatest coverage in this community type and could be considered a characteristic taxa here. *Myrica gale* is the most common shrub but is not abundant. It and *Alnus crispa* occur only in narrow, linear stands along the uppermost channel bank. *Salix commutata* is more abundant than *S. barclayi*, and a few *S. stichensis* are sympatric with *A. crispa*. The prostrate *S. arctica* is common in the ground layer.

Habitat—This community type is present on the highest elevation (5.4 ± 0.2 meters) and most inland habitat of the Eyak River Marsh. Although the levee was formed by water-deposited sediments, this process no longer occurs at the levee's present elevation above sea level. Tidally raised, heavily sedimented fresh water enters the channel immediately adjacent to the levee. It is easily identified because it is grey and opaque in contrast to fresh water draining the marshes, which is clear although discolored by transported and dissolved organic materials. Even with possible higher surface water levels due to channel constriction, the levees currently are not inundated by even the highest spring tides.

The levees occasionally may be flooded during periods of intense rainfall if the water level in the adjacent ponded basin rises sufficiently. Rainfall also may be so intense that the substrate of the levee cannot absorb all the water and floods temporarily. Lateral surface drainage into the channel occurs in this situation. This process may be more common than is readily evident. Low-altitude, oblique-angle aerial photographs taken before plant growth starts in the spring show a continuous series of small lateral erosion rills oriented at right angles to the levee axis draining into the channel. These are well vegetated, and direct erosion of the substrate is not common. This is fortunate because the substrate is highly erodible. Waterfalls in artificial channels that cut through similar levees in other areas of the Copper River wetlands for pond drainage soon develop deep (2 to 3 meters) plunge pools and show severe headcutting erosion. This occurs even though the substrate has a great volume of roots incorporated into it.

The surface of the levee appears to be raised above that of the adjacent interlevee basin. Exact differences in elevation are difficult to determine because of the thick cover of litter and cryptogamic vegetation.

A standing water table always existed in the substrate; the height of it depended on the level of the water in the adjacent ponded basin. Water seems to move slowly and laterally in the organic layer and upper portion of the inorganic substrate, which has a platy (or varve) structure. As on the seaward bank of the foreshore levee, small springs and seeps are common on the channel bank of the interior levee. Because of the year-long high water table, the interior levee is a true wetland; however, the slightly higher surface elevation and the fluctuating water table allow the surface portion of the levee substrate to be better aerated than that of the ponded basin. This may partially account for the abundance and species richness of the vegetation.

C-T8: *Carex/Lathyrus* C-T on moderately hydric interlevee basin habitats (7 stands)—

Structure—A multistrata, graminoid-dominated meadow characterizes this community type. The taller herbaceous stratum is 40 to 60 centimeters tall and predominantly sedge. Grasses are relatively common, well distributed, and equal in height to the sedge. Clambering forbs are common in the lower herbaceous stratum and can be so abundant as to impede walking. The ground stratum is covered with a dense cover of litter and cryptogamic taxa. Total coverage by vascular plants is 135.6 percent; graminoid coverage, 92.7 percent.

Composition—*Carex lyngbyaei* is the most abundant taxon and *Calamagrostis canadensis* is the most common grass, but *Festuca rubra* and *Deschempsia beringensis* are widely distributed. The clambering forbs are *Lathyrus palustris* and *Galium trifidum*. *Equisetum arvenses* and *Athyrium filix-femina* are locally abundant. *Epilobium hornemannii* is widely distributed but grows mainly in the lowest stratum. *Cicuta douglasii* is common but depauperate.

Habitat—Stands representative of this community type are present throughout the poorly drained interlevee basins. The dense herbaceous vegetation made it impossible to accurately determine the degree, shape, and direction of the surface configuration, but in general it is flat to very slightly upward sloping toward the adjacent foreshore, interior levee habitats, and stands of the *Carex/Lathyrus* C-T located on the outer periphery of the interlevee basin.

Except after periods of very intensive rainfall or recent snowmelt, a supersurface water table usually is not present. The subsurface water table usually is close to the upper surface of the litter-cryptogam stratum, and this remains saturated throughout most of the growing season.

The high water table and the dense, relatively tall plant cover keep the relative humidity of the lower plant strata very high, even after several days without precipitation.

The actual water level fluctuates with the pattern of precipitation and may be as much as 10 to 15 centimeters under the surface. The litter-cryptogam stratum grades imperceptibly into saturated organic muck, which in turn grades into an organic-inorganic substrate at depths of 0.5 meter or more. The inorganic material is water-deposited glacial silt. Core samples from the deeper layers of the substrate have a distinct odor of hydrogen sulfide; anaerobic conditions with chemical reduction processes are assumed to be present. The near-surface layers are assumed to be aerobic owing to the fluctuating water table.

C-T9: *Cicuta/Carex-Lathyrus* C-T on hydric interlevee basins (8 stands)—

Structure—The vegetation structure of this community type, is quite similar to that of the Carex/Lathyrus C-T except that a well-developed tall herb stratum of water-hemlock (*Cicuta douglasii*) is present late in the growing season. This stratum can exceed 2 meters in height but usually is about 1 meter tall. Differences in height seem to be related to environmental differences in the growing seasons, but the environmental variables controlling growth are not known. As height increases so does canopy coverage, which can more then double in good growth years. In the fall, water-hemlock is inconspicuous. No shrubs are present. The herbaceous and litter-crytogam strata are much the same as those of the *Carex-Lathyrus* C-T. Total canopy coverage of live vascular vegetation was 120.5 percent.

Composition—*Cicuta douglasii* is the sole member of the tall herbaceous stratum. *Carex lyngbyaei, Festuca rubra,* and *Deschampsia beringensis* are the most important graminoids, and *Lathyrus palustris, Eguisetum arvense*, and *Epilobium hornemannii* are the more abundant forbs in the lower herb strata. In general, although fewer of the major forb taxa are present in the lower herbaceous strata, the overall composition is quite similar to the *Carex-Lathyrus* C-T.

Habitat—Stands representative of the *Cicuta/Carex-lathyrus* C-T occupy the wettest habitats in the old marsh. They occur on concave microtopography in swales and vegetated watercourses along the periphery of shallow wetland ponds. Water forms ponds on the surface in these locations for long periods after snowmelt or intense precipitation. A permanent supersurface water table may be present but is hard to detect because of the dense, thick litter and cryptogamaic strata. The vegetation on these sites, particularly the sedge, tends to become green somewhat earlier in the growing season then at other locations in the interlevee basin. The substrate is quite similar to that found under the *Carex-Lathyrus* C-T. The major difference was the presence of the large, chambered roots of *Cicuta douglasii*.

Discussion

Phytosociology

A large degree of floristic similarity exists among the nine community types. Most characteristic taxa are present in most community types. Differences are due to shifts in canopy coverage and constancy rather than distinct changes in taxa composition, and all the community types might be considered as variants of a sedge-dominated vegetation type. Although taxa composition is comparable, similarity coefficients based on the modal values of the attributes indicated, however, that the community types are relatively dissimilar (fig. 6). The maximum reciprocal similarity coefficient between two community types is 64.4 percent, and only 6 of 36 similarity coefficients exceed 50 percent.

Cluster analysis sorted the nine community types into two major sections corresponding to the floristically simple, sedge-dominated tidal marshes and the more species rich nontidal marshes. The sections joined at a similarity of only 32.6 percent. The tidal habitat section contains only three of the four community types developed in the cluster analyses based on the similarities of individual stands. The *Myrica/Carex* C-T of the highest levee habitats was placed in the nontidal habitat section. This section had two subsections: one for the community types of the interlevee basin and interior levee and the other for the shrubby foreshore levee community types. The *Myrica/Carex* C-T was clustered in this last subsection.

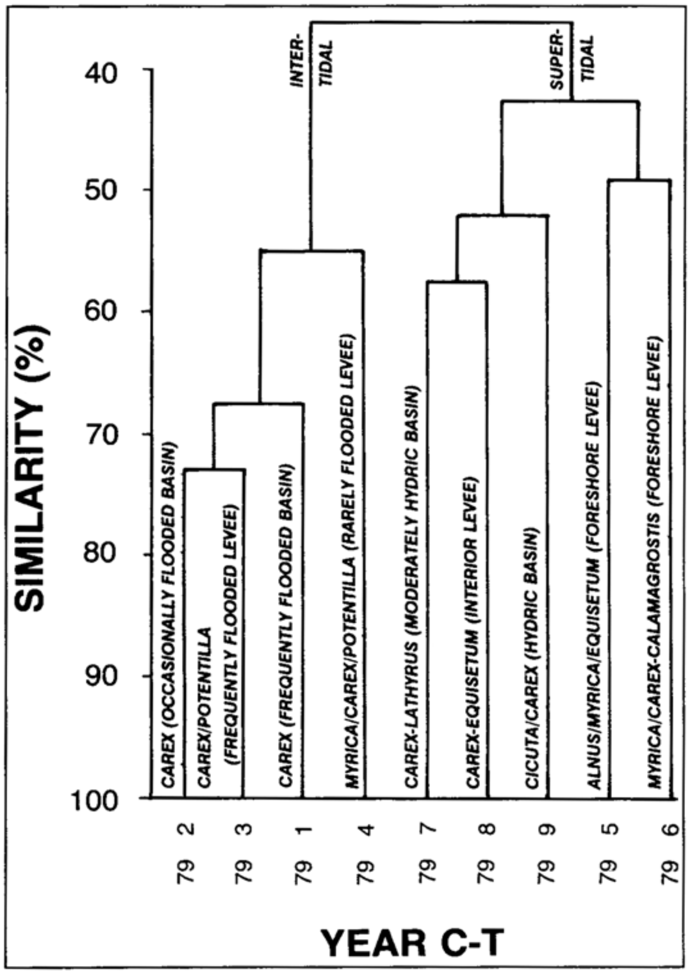

Figure 6—Dendrogram of the similarities of the nine community types of 1983 based on the modal values of the attributes in 1979.

In the tidal habitat section, the *Carex* C-T of both high and low new marshes were 64.4 percent similar, the highest level recorded. The *Carex/Potentilla* C-T of low levees joined these at a similarity of 52.5 percent.

Community types are not static entities; they represent points or stages in a time-related continuum as well as on a habitat-influenced continuum. The similarities and relations in 1979 of the community types defined in 1983 are shown in figure. 7. The dendrograms for the two periods are much alike. The major differences are the location of the *Carex/Myrica* C-T in the tidal habitat section; the changes in the reciprocal similarities of the sedge-dominated community types in this section, and a slightly higher level overall of similarity between all community types in 1979.

The shift of the *Myrica/Carex* C-T between 1979 and 1983 is due to a large increase in the canopy coverage of *Myrica gale*. During the 4-year interval, *M. gale* expanded its distribution seaward and increased in canopy coverage in place. Mean canopy coverage of *M. gale* increased from 3.6 to 87.2 percent in the *Myrica/Carex* C-T and from 0.8 to 5.8 percent in the *Myrica/Potentills* C-T between 1979 and 1983.

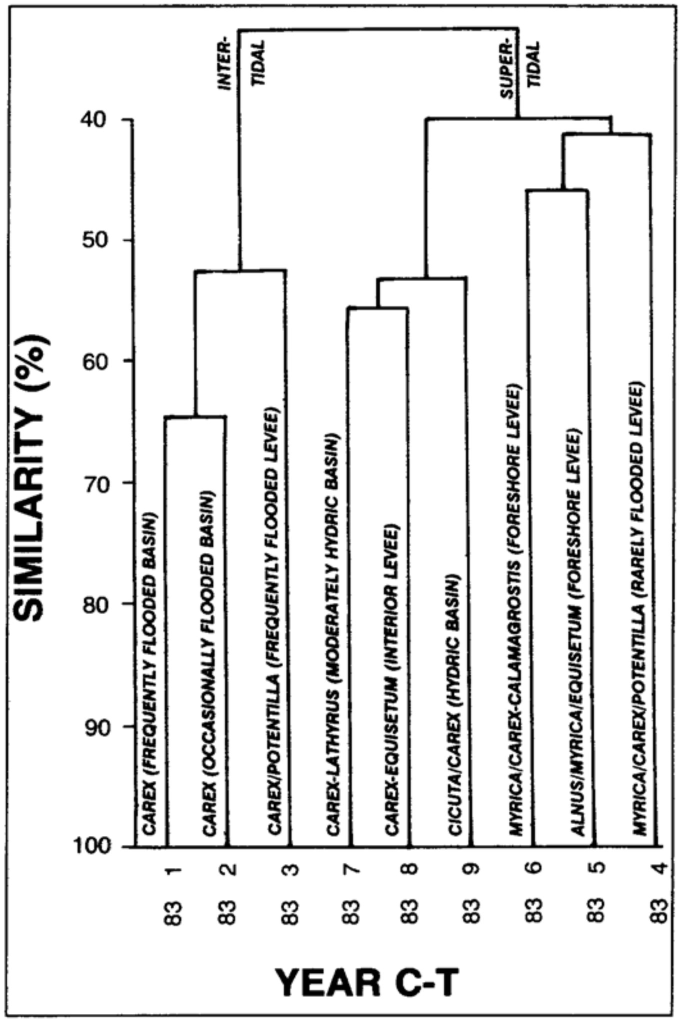

Figure 7—Dendrogram of the similarities of the nine community types of 1983 based on the modal values of the attributes in 1979.

Stands of the *Carex/Potentilla* C-T may evolve into the *Myrica/Carex* C-T in the near future. Similarly, the *Myrica/Carex* C-T may evolve into the related *Myrica/Carex-Calamagrostis* C-T of the adjacent foreshore levee habitat.

With the exception of the move of the *Myrica/Carex* C-T, no analogous changes in community type interrelations occurred in the nontidal habitat section. The shrub-dominated foreshore levee community types retained the same interrelation to one another, as did the herbaceous community types of the interior levee and basin. In 1979 and 1983 the *Carex-Lathyrus* C-T of the interior levee were more similar to each other than to the *Cicuta/Carex-Festuca* C-T of the hydric interlevee basin habitat.

Unfortunately no quantitative information on the development of the Eyak River Marsh is available before 1979. The best available information on the pre-1979 vegetation is the 1:15840-scale Ektachrome aerial photography of June 22, 1974 (fig. 2), which show a relatively complete cover of graminoid vegetation, presumably *Carex lyngbyaei,* extending 300 meters seaward of the foreshore levee and lines of similar vegetation growing closely parallel to tidal creeks and drainage channels to a distance of over 1200 meters from the foreshore levee. A few scattered clumps of vegetation are visible beyond 1200 meters, but the full seaward extent of their distribution cannot be determined because of the level of the tidal water when the photograph was taken. The shadow line on the mountain slope to the west indicates the photograph was taken in midafternoon. The 1964 tide table indicates an ebbing tide from a 3.1-meter lower-high water level, and on the basis of the elevation survey made in this study, the tide line would have been near 1.0 meter above mean sea level.

Primary Succession

Low-elevation (ca 150-meter) oblique photographs taken in 1981 (fig. 8) illustrate the developmental patterns of tidally influenced sedge meadows. The sequence is single plants, tussocks, patches, individual rings, coalescing rings, and linear clumps located predominately on the inside curves of the levees paralleling the channels. These combine into linear bands and then spread along both sides of the channel and outward into the slightly lower elevation interlevee basins.

Ring formation seems to be a constant and common feature of the invasion pattern. The rings persist after the full tidal meadow develops. They are easily seem from an aircraft at low elevation, especially when the sun is at low angle, but usually cannot be seen by an observer on the ground.

The pattern of invasion of the earthquake-uplifted tidal flats by the sedge *Carex lyngbyaei* is remarkably the same as that described for the grass *Spartina townsendii* on the tidal flats in England (Hubbard 1965, Oliver 1925). The root systems of *S. townsendii* and *C. lyngbyaei* also are quite similar. Both have deep anchor roots extending far into the substrate and a mat of stolons and finer roots within the upper few centimeters of the substrate.

As in *S. townsendii*, the center of the *C. lyngbyaei* ring is not barren; rather, it has less dense and shorter culms. Peripheral culms are not only tailer than the central culms but also appear more vigorous with their darker green color.

There is greater accumulation of sand in the peripheral ring than in the center. Surface accretion consequently proceeds faster there. An informal study of accretion rate in one ring of *C. lyngbyaei* showed a mean total accretion of sediments in the ring periphery of 11.2 $\pm$ 0.8 millimeters and 5.8 $\pm$ 0.7 millimeters of sediments in the center of the ring. On bare substrate immediately outside the ring, 1.0 $\pm$ 0.2 millimeter of sediment accreted. This study ran over five mixed diurnal tidal cycles with tide levels from -0.6 to 3.6 meters. The site was 1.1 meters above sea level.[4]

Successful establishment of *C. lyngbyaei* at the outermost limits of vegetation is unknown. Flowers and seed are produced each growing season, but the vitality of the seed and the requirements for seed germination and seedling establishment are not known. Single culms of *C. lyngbyaei* are present on levees 1.8 kilometers out into the tidal zone. These seem to have developed from seeds, but only aerial shoots from stolon were examined, and they were connected to other shoots or well-developed plants.

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[4] Unpublished data: On file with: John F. Thilenius, Juneau, AK.

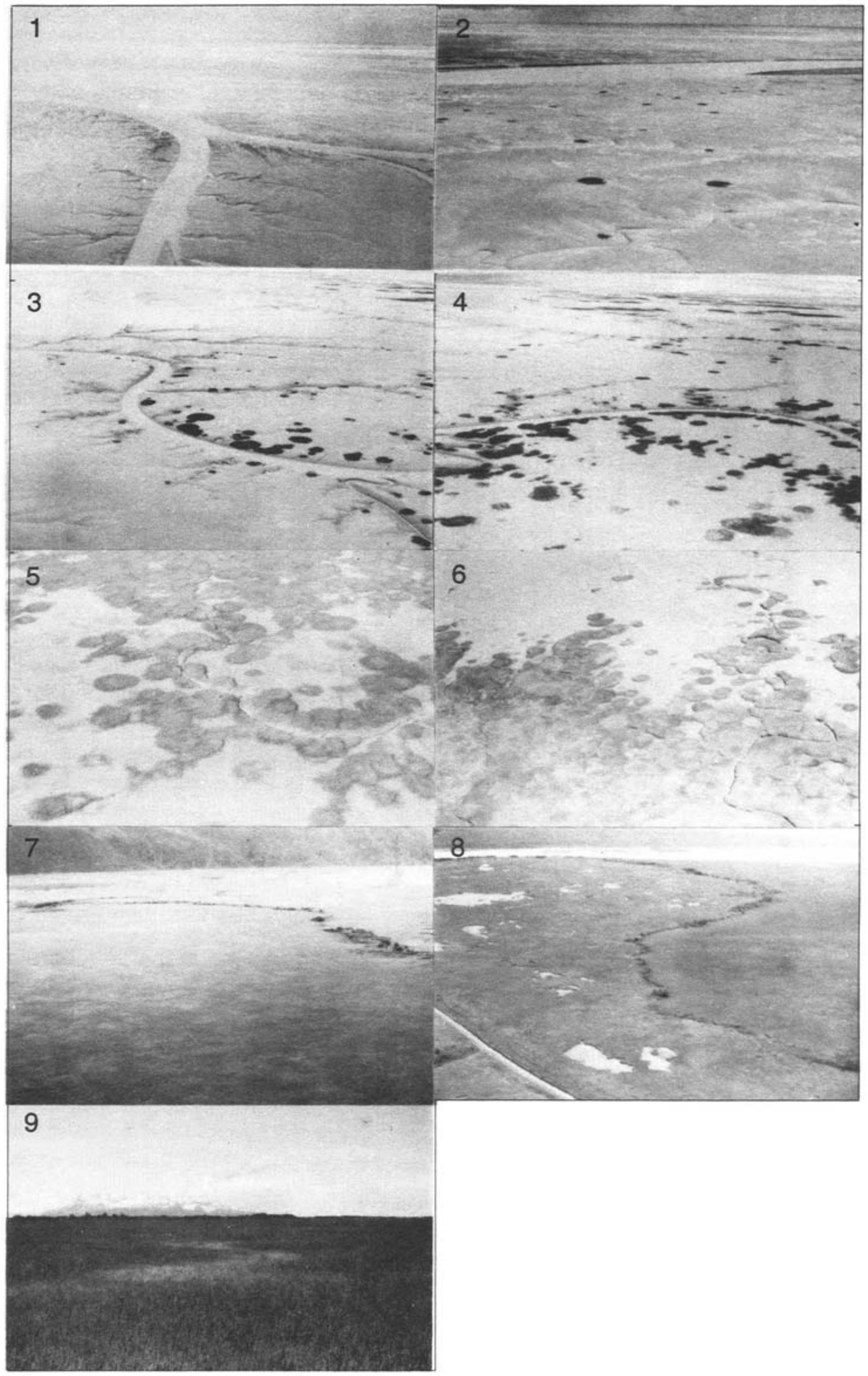

Figure 8—Developmental patterns on tidally influenced sedge meadow: 1—barren tidal flats; 2—initial colonization; 3—sedge rings on tidal creek levee; 4—increasing density of sedge meadow; 5—coalescing rings; 6—initial meadow; 7—tidal sedge meadow; 8—tidal sedge meadow to left, formerly tidal marshland to right; and 9—ground level view of sedge marsh.

The sediment of the outer tidal flats tends to crack into roughly five-sided polygons when the surface dries. These cracks seem to be more-or-less permanent features. They close when wetted by tidal water or precipitation and reopen when again dried. The stolons of *C. lyngbyaei*, and also those of the grass *Puccinellea phryganodes*, spread horizontally along these zones of sediment weakness. Aeration is better in the cracks, as is available water. A lack of available water seems an anomaly in a frequently flooded tidal flat, but because the fine silt and glacially derived sediments (claylike but but not true clays) pack so tightly there is little available water or water movement in the sediments. Without tidal flooding or rainfall, holes left after the extraction of substrate sample cores do not fill from ground water after 24 hours or more, even when cores have been extracted from a location with standing surface water. A raised edge 1 to 2 centimeters high is left around the surface periphery of the corehole in the process, and this prevents free surface water from flowing into the hole. The substrate at depth in the cores becomes only damp, and free water does not appear when the extracted cores are allowed to stand for several hours.

The surface of the tidal flat is a gellike suspension of sediments that is very smooth and slippery when wet. Sediment adheres to but does not accumulate on boots (or the feet of geese, brown bear, and moose). Walking across the tideflats leaves a series of shallow, dry tracks, and the impressions may remain visible for several weeks. The surface may have a relatively low coefficient of friction, and turbulence at the tidal water-substrate interface may be very low. The minimal accumulation of sediments on the tideflat adjacent to the sedge ring (mentioned above) indicates this. Even though the surface is slippery, the densely packed subsurface sediments provide firm footing except in small drainage channels and along the banks (but not on the levees) of major channels. Where the sediment becomes quicksandlike, it is possible to become bogged down.

The other method by which plants may establish on the outer flats is fragmentation. The presence of sod islands with a complement of upland taxa on the tideflats was discussed above. Fragmentation also can be brought about by wave action, and *C. lyngbyaei* plants may be broken loose and transported by waves during both the dormant and growing seasons.

The winter storms of the Gulf of Alaska are well know for their strength. Storms during the growing season are not usually as intense, but severe storms with winds to 164 kilometers per hour and intensive rainfall (ca 400 millimeters in 24 hours) occurred during summer while this study was in progress. Under such conditions, strong wave action is present even inside the barrier islands. The barrier islands now are about 9.6 kilometers offshore of the foreshore levee, and a long wind fetch is present. In addition to uprooting and transporting plants, waves can move many natural and manufactured objects. Because any object on the surface of the tideflat will alter laminar flow to turbulent flow and create a consequent zone of deposition in its lee, storms may be both destructive and constructive in their impact on the habitat and on the plants that may establish and grow there. As in most tidal marshes, the vegetation at the seaward edge is subjected to continuous disturbance of its habitat and itself. The floristically simple *Carex* C-T must be regarded as being in a continuously disturbed stage of development. At the Eyak River Marsh, the greatest range in tide levels occurs from November through January, when the marsh surface is frozen and covered with ice or snow, although high-velocity winds often remove the snow cover and wintertime thaws do occur. River runoff from the Copper River and other local rivers is at its lowest because the glacier melt rates are low and precipitation comes mainly as snow.

Considerable fresh water also is held as lake and river ice. Because of the reduction of freshwater input and the presence of high tides, strong onshore winds, and low atmospheric pressure from the frequent storms of the Gulf of Alaska, saline water penetrates farther inland in winter when it covers frozen surfaces and dormant vegetation.

Just as the amount of fresh water is reduced, so is the amount of sediment transported in this water. Sediment input is directly related to the rate of melting of the glaciers. In winter this is low and the water from the glaciers is relatively, but not completely, clear. Secchi transparencies are 1 to 2 meters.

The onset of significant glacial melting differs from year to year but usually begins in early to mid June. The onset is rapid and the sediment load increases at a high rate. Secchi transparencies can decrease to below 1 decimeter in less than 24 hours. Once meltwater runoff starts, the rivers remain highly turbid until late fall. The greatest rate of river runoff occurs from late July to early August, when the ocean surface several kilometers seaward of the barrier islands is covered with turbid fresh water. Although the water is extremely high in transported sediments, it is very low in dissolved ions. Conductivity is usually less than 50 millimohs per square centimeter in rivers originating in glaciers. In water originating in the upland marshes, it is in the range of 600-700 millimohs per square centimeter. Water temperature in rivers rarely exceeds 6 °C, but the water flowing from marshes may be 20 °C or more on sunny days. In contrast to the opaque gray glacial water, water from the marshes is relatively clear (Secchi transparency > 1meter), but is stained an olive brown color, presumably by organic matter. No information is available on specific inorganic and organic matter content for either type of water.

A well-defined saltwater wedge is present in the Eyak River in summer.[5] At the slack of a higher high water of 4.0 meters, salinity was 2 ‰ at a depth of 6.0 meters in the main channel of the Eyak River about 30 meters seaward of the foreshore levee. During summer, the water flooding the marsh at the base of the foreshore levee to a depth of 20 centimeters was fresh. About 20 minutes later, a bottom salinity of 4 ‰ was obtained about 1200 meters from shore (over a stand of the *Carex* C-T at 1.1. meters elevation). The surface water was still fresh. Spring tides of 4.0 meters occur four to five times from May to September. At the lower low water (-0.5 meters) of the same spring tide cycle, only fresh water was present in the main river channel 2 kilometers seaward of the foreshore levee. At higher high water, the salinity was 23 ‰.

Abundant summer rainfall and low evaporation due to a high incidence of cloudiness with consequent low direct insolation keep salinity of the substrate water in the low new marsh at meso-mixo haline to fresh levels. Substrate salinity ranges greatly, however, over horizontal distances of a few meters and is partly dependent on the particle

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[5] Hazardous weather and sea conditions prevent winter measurements.

size of the sediments. Coarse sediments allow greater penetration of the flooding water, but also drain rapidly and are flushed by rainwater. Tightly packed silts, which comprise most of the substrate away from the levees, resist the penetration of tidal water.

Direct evaporation of substrate surface moisture takes place during periods of sunshine when the wind blows offshore. On the barren tidal flats and pans at the outer edge of the marsh, dense clouds of water vapor 1 to 3 meters high form over unvegetated areas in this type of weather but not over immediately vegetated sites. Substrate and substrate water salinity of these barren locations are not significantly different from those of the adjacent vegetated areas.

In general, even the most seaward parts of the marsh must be considered as only moderately brackish habitat. Crow (1968), Jefferson (1975), and Moody (1978) all indicate one dominant plant of this part of the marsh, *C. lyngbyaei*, is not well adapted to saline environments. Its distribution across the Eyak River Marsh also indicates this. It is abundant in tidal habitats but also grows well in the nontidal, old marsh habitats. Ranwell (1972) indicated that long-term inundation by tidal water was not, by itself, limiting to the survival, growth, and distribution of tidal marsh plants, but constant and extreme water turbidity could be by limiting the light available for photosythesis. Information on the attenuation of the photosynthetically active wave lengths of light by clear water is readily available (Williams 1962); published information on light reduction in turbid waters is less available.

In rivers classed as very turbid (Westlake 1966), the percentage of light available at a depth of 1 meter ranges from 0.6 percent to negligible of that at the surface. “Very turbid” was not defined. The data were obtained by direct measurement with selemium photocells, but Westlake reports on the work of others who used Secchi disc measurements to estimate the percentage of light at depth in turbid water. Reid (1961) indicates the Secchi disk will disappear in the region where light transmission (all wave lengths) is reduced to 5 percent of that impinging on the surface. At the Eyak River Marsh the average depth of 20 Secchi disc disappearances was 1.04 + 0.11 decimeters.[6] These data were taken at lower high water in the river and on adjacent flooded marsh. Little light is available for photosynthesis if the plant is flooded to a depth of 1 decimeter above its total height. Most *C. lyngbyaei* do not exceed 4 decimeters in total leaf height. Taller plants are present along the levees and well into the outer marsh zone; however, these are often lodged by the strong winds or tidal currents. The leaves of *C. lyngbyaei* growing on frequently inundated locations often are so completely coated with adhered silt that the green color is almost obscured. This coating may further limit the ability of the plants to photosynthesize. The silt adheres tightly to the leaves and is not easily removed by precipitation. Lodged live culms may be completely buried by sediment deposition further reducing photosynthetic surface.

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[6] Unpublished data. On file with: John F. Thilenius, Juneau, AK.

Table 3—Calculated exposure period for the May 15 to September 15 growing season expressed as a percentage of total hours not flooded at 0.5-meter-elevation increments between -1.5 and 4.0 meters

Elevation	Period exposed (percent of 3000 hectares) Day	Night	Total	Times exposed
Meters		*Percent*		
-1.5	0	0	0	0[a]
-1.0	.3	0	.3	6
- .5	2.2	T[b]	2.2	27
.0	10.6	T	10.6	70
.5	23.2	1.9	25.2	113
1.0	36.3	5.9	42.1	165
1.5	45.7	9.9	55.6	186
2.0	55.3	13.0	68.3	187
2.5	65.0	16.1	81.2	150[c]
3.0	71.4	20.1	91.5	93
3.5	73.6	24.3	98.0	33
4.0	73.8	26.0	99.9	5[d]

[a] Always flooded below -1.5 meters.
[b] Less than 0.1 percent.
[c] Exposed flooded at > 2.5 meters and higher.
[d] No flooding at elevations > 4.2 meters.

In addition to water turbidity, exposure of the plant during daylight hours is critical. From May to September, lower tide levels at the Eyak River Marsh coincide with daylight hours (see table 1) and the photoperiod from May through July is quite long (table 3). This is also the period of greatest cloud cover with a high incidence of rainfall and fog. Stratus and nimbostratus clouds often accompanied by heavy rains are the most common cloud types present. These clouds transmit, respectively, 25 and 19 percent of clear sky radiation; only 17 percent of solar radiation is transmitted through fog (List 1966).

The absence of plant species adapted to saline water (for example, *Salicornia europea, Suedea depressa*) and the low abundance of other halophytic taxa (*Puccinellia* spp., *Triglochin* spp.) are indicative of low salinity. The seaward expansion of *C. lyngbyaei* may be controlled by a combination of daylight period and water turbidity other than salinity. Moody (1978) found *C. lyngbyaei* on the Fraser River tidal marshes in British Columbia to be most abundant at an elevation exposed 53 percent of the time in daylight hours during an April to September growing season. The outer limit of *C. lyngbyaei* distribution was an elevation exposed 46 percent of the time in this period. She did not measure onsite water turbidity but did state that Fraser River water was “murky brown,” indicating some degree of turbidity was present.

At the Eyak River Marsh, comparable exposure (during a growing season 1 month shorter) occurs at elevations of 1.9 meters (53.7 percent daylight exposure) and 1.5 meters (45.7 percent daylight exposure). Most of the closed canopy sedge meadow is above 1.7 meters elevation (49.4 percent daylight exposure), detached clumps and rings occur at lower elevations, and scattered tussocks and individual plants are found up to 0.5 meter elevation (23.3 percent daylight exposure).

Secondary Succession

The preceding discussion dealt with primary succession and phytosociological development on the new marsh habitats unoccupied by vascular vegetation before the 1964 uplift. A well-developed vegetation was present on old marsh habitats before the earthquake, and uplift vegetation changes there are properly secondary succession. None of the available information on the preearthquake (Trainer 1959) and immediate postearthquake wetland vegetation (Crow 1968, 1971, 1976) of the Copper River Delta was collected in the old marsh habitat at the mouth of the Eyak River, and only photographic evidence is available for the years before 1979. Fortunately, the scale and quality of the 1974 aerial photographs are excellent, and much can be interpreted about the old marsh vegetation as it was 16 years after the uplift.

It is evident from the photographs that most of the foreshore levee now occupied by stands representative of the *Alnus/Myrica-Salix/Carex* C-T and *Myrica/Carex-Calamagrostis* C-T were almost without shrubs in 1974. Only the immediate western bank of the Eyak River inland (north) from its preearthquake mouth had a continuous stand of shrub vegetation at that time. These shrubs can be identified from color and crown shape as *Alnus crispa*. From the length of the shadow they cast, the tallest individuals were about 3 meters high and the stand of shrubs was less than 4 meters wide. Vegetation on this site is the *Alnus/Myrica/Salix/Carex* C-T.

Scattered *A. crispa* and a few *Salix* spp. also were present along the foreshore levee to the west of the mouth of the river. By 1983, this area was occupied by stands of both shrub community types along almost its entire length and width. In 1974 no shrubs were present on the tidally influenced high levee immediately below the foreshore levee. In 1983 the *Myrica/Carex* C-T occurred here, and the canopy coverage of *Myrice gale* exceeded 87 percent.

In 1974, only a few scattered shrubs of *A. crispa* and *Salix* spp. were present on the interior levee where it merged into the foreshore levee at the mouth of Center Slough, but both channel banks were free of shrubs. By 1979, narrow, linear groves of *A. crispa*, *M. gale* and a few *Salix* spp. were present at and below the abrupt change in the surface topography where the levee slopes into the channel. Only a few *M. gale* were present on the upper surface of the levee. The shrub component of the interior levee vegetation was much the same in 1983, when a nonsignificant decrease in canopy coverage by all shrub taxa was recorded.

The light texture in the photograph indicates grasses as the predominant vegetation for the upper surface of both the foreshore and interior levees in 1979. Stands of dried grass stalks, and especially grassleaf litter, have this distinctive look in the early part of the growing season when the aerial parts of the current years growth of herbaceous plants are just emerging through the litter layer. Under magnification, the lateral erosion rills on the grass-covered channel banks are visible in the photographs.

The interior levee vegetation still had a dry grass meadow aspect in the early growing seasons of 1979 and 1983, but by late July to early August (when sampling occurred), forbs and *Carex lyngbyaei* had developed sufficiently to alter the appearance to a mixed forb-sedge meadow.

The 1974 aerial photographs indicate that the interlevee basin was a sedge meadow. In 1979 and 1983, stands of the *Cicuta/Carex-Festuca* C-T may have been present but cannot be detected on the photographs because the flowering stems of *Cicuta douglassii* do not develop fully until August. These stems may exceed 2 meters in height when alive, but when dried, they are fragile and easily broken and removed by wind. As with many herbs, large differences occur in the growth of *C.douglassii* from year to year.

Most stands of the *Cicuta/Carex-Festuca* C-T occur next to the edges of the shallow ponds clearly visible on the photographs. Stands of the *Carex-Lathyrus* C-T now occupy most of the interlevee basin. This community type is more closely related to the *Carex-Equisetum-Lathyrus* C-T of the interior levee habitat than it is to the *Cicuta/Carex-Festuca* C-T. Overall, the community types of the interlevee basin seem to have changed the least after the uplift.

Wetland meadow vegetation types similar to those of the interlevee basin habitat at the Eyak River Marsh apparently were present in interlevee basin habitats elsewhere on the Copper River Delta in 1966 (Crow 1968) however, the descriptions of the wetland meadow vegetation types were not based on quantitative data, so direct comparisons cannot be made. Crow’s community types are the only available information on the immediate postearthquake vegetation on the levee habitats of the western Copper River Delta wetlands. The classification is detailed and stresses environmental differences as controlling influences, but it has some limitations. It is based on the classification method of Daubenmire (1959) in which stands of vegetation that appear to an observer to be compositionally similar and spatially repeated are subjectively selected and mentally abstracted into phytosociological classification units. Taxa composition and canopy coverage are sampled only to provide descriptive criteria, not to develop classification units. Further vegetation (and site) attributes from sampled stands are not combined into generalized descriptions of the classification units.

Disregarding the subjective development of the classification units, but applying the criteria of major underlying environmental differences and the necessity to have multiple samples to provide adequate descriptive criteria for classification units, it appears that only four major wetland vegetation types were described for the levee habitat in 1966:

1. A forb-grass vegetation on the most seaward levees that were occasionally inundated by tidal water under preearthquake conditions.
2. A low shrub-grass vegetation on levees slightly more inland, and much less likely to be flooded by tidal water, than the levees in number 1, above.
3. A mid-shrub/grass-forb vegetation on still more inland levees that received only river floodwater inundation even before the earthquake.
4. A tall shrub-grass vegetation on the most inland levees flooded only occasionally by river overflow.

None of the other wetland community types described in 1966 (for example, sedge-dominated tidal marsh communities and interlevee basin sedge marshes) is supported by data.

Crow (1968) did not calculate modal attribute values to describe the community types of levee habitats present in 1966, but the published data allow this to be done. The modal values and constancy for taxa with an average canopy coverage of 10 percent or more are given in table 4. To facilitate comparison with the 1983 community types, the names of the 1966 community types have been revised to agree with the system used in this study.

The community types of 1966 were structurally similar to those now present. There was a species-rich levee community type where herbaceous taxa predominated and three community types where shrubs formed well-defined strata above herbaceous vegetation. The same three shrub taxa were important in both 1966 and 1983. The most important compositional differences were the complete absence of *Hedysarum alpinum* from the Eyak River Marsh and the much reduced canopy coverage of *Carex lyngbyaei Hedysarum alpinum* currently is present and relatively abundant in levee habitats east of the Eyak River, and although the exact locations of the stands Crow sampled in 1966 are unknown, it is thought most were east of this area.

Even the most seaward of the levees to the east have a more inland location than those of the Eyak River Marsh because of the location of the offshore barrier islands and the orientation of the distributary channels of the Copper River and local glacial streams. These levees also may be at a higher elevation. During lower low water periods of spring tides, the tidal flats between the outermost levee and the offshore barrier island can be completely exposed. This does not occur at the Eyak River Marsh.

The more inland position and higher elevation could mean a reduced frequency of tidal flooding of the eastern marshes in the preearthquake period compared to the Eyak River Marsh. A long-time (ca 70 years) resident of a fishing village (now a recreational cabin site) from the east bank levee of the Eyak River immediately opposite the Eyak River Marsh indicated flooding of the levees there was a common occurrence before the earthquake.[7] It is possible that what is now the old marsh portion of the Eyak River Marsh received much more frequent and longer duration inundation before the uplift. This could account for the current abundance of *C. lyngbyaei* and lower coverage of true grasses throughout the present vegetation and might also account for the absence of *H. alpinum*.

The more protected eastern levees of the Copper River Delta also may be of greater geological age, and the vegetation there is in a more advanced stage of succession than on the newer western levees. Reimetz (1966) found buried stumps and wood of *Picea sitchensis* at two levels beneath the present marsh surface. The upper of the two layers was carbon dated at 700 years BP, the lower at 1750 years BP. In-place tree stumps are present in the upper reaches of the channel of Center Slough 4.3 meters below the marsh surface, and similar stumps are exposed at low tide at the base of the bank along the Eyak River. The presence and abundance of *H. alpinum* on fine-textured substrates in marshlands near sea level is in itself of interest. According to Hultén (1968) and Welch (1974), it is a plant of “rocky slopes, spruce forest and gravel bars” in the boreal forest, taiga, and arctic and alpine tundra throughout Alaska and Canada.

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[7] Personal communication. James “Ed” King. ca 1980.

Table 4—Stand taxa composition and percentage of coverage and frequency for the most abundant taxa of the community types of levee habitats in 1966

Species	Percent coverage	Range coverage	Percent frequency
Deschampsia/Potentilla (ex *Hedysarum-Deschampsis*, and *Hedysarum-Equisetum* C-T) 12 stands:			
Deschampsia beringensis	56.4	(20-83)	100
Potentilla egedii	46.9	(10-79)	100
Triglochin maritinum	30.9	(0-81)	92
Hedysarum alpinum	30.3	(2-77)	100
Festuca rubra	29.4	(1-75)	100
Carex lyngbyaei	25.8	(4-70)	100
Plantago macrocarpa	17.5	(0-48)	92
Lathyrus palustris	11.9	(2-31)	100
Myrica/Festuca (ex *Myrica/Poa* and *Myrica-Hordeum* C-T) 7 stands:			
Mrica gale	82.0	(64-93)	100
Festuca rubra	66.0	(37-96)	100
Poa eminens	38.9	(0-69)	86
Deschampsia beringensis	23.9	(6-42)	100
Potentilla egedii	10.4	(2-27)	100
Salix/Equisetum (ex *Salix/Festuca*, *Salix/Equisetum* and *Salix/Calamagrostis* C-T) 7 stands:			
Salix spp.[a]	73.4	(35-98)	100
Equisetum pratense	69.0	(7-98)	100
Myrica gale	35.4	(0-90)	71
Festuca rubra	28.7	(0-90)	71
Sanguisorba stipulata	22.4	(0-45)	86
Lathyrus palustris	13.6	(0-46)	86
Calamagrostis inexpansa	12.4	(0-26)	86
Alnus/Calamagrostis/Equisetum (ex *Alnus/Calamagrositis* and *Alnus/Arctagrostis* C-T) 4 stands:			
Alnus crispa	75.5	(48-93)	100
Calamagrostis canadensis	47.0	(0-96)	75
Equisetum pratense	45.5	(6-94)	100
Salix spp.[b]	22.3	(6-42)	100
Arctagrostis arundinacea	16.3	(0-42)	50

[a] *Salix barclayi* or *S. commutata*. Crow did not distinguish the species of willow.
[b] *Salix sitchensis* is the willow species most commonly sympatric with *Alnus crispa*.
Source: Developed from Crow 1968.

The understory taxa of the three 1966 community types having well-developed shrub strata were present in the understory of shrub community types in 1974 and 1983. The relative abundance of individual taxa was not the same. *Carex lyngbyaei* was the characteristic taxa in the two 1974 and 1983 shrub community types on the old marsh, but both *Calamagrostis canadensis* and *Equisetum* spp. also were abundant. *Arcatagrostis arundinacea* was not recorded.

A direct analog of the *Salix/Equisetum* C-T of 1966 was not present in the Eyak River Marsh in 1983. A zone of shrub vegetation with *Salix barclayi* predominant in the upper shrub stratum presently covers thousand of hectares on coarse-textured glacial outwash plains 6 to 8 kilometers inland from the foreshore levee. Shrubland dominated by *Alnus crispa* is present but confined to the immediate banks of water courses. A few widely scattered *A. crispa* also are present in *Salix/Myrica* shrubland.

Both Trainer (1959) and Crow (1968) emphasize the presence of distinct bands or vegetation.zones of shrubland dominated by either Salix spp. or A. crispa, or both, in the more inland zones and either low shrub (*Myrica gale*) or herbaceous vegetation on the seaward levee. Since the 1964 uplift, this well-defined zonation has become much less distinct, although it still can be identified. The same three major species of shrubs have extended their distribution to the outermost levees.

In the immediate postearthquake period, the term “willow invasion” was commonly used. In more recent times, this has changed to “myrica (or sweetgale) invasion” and “alder invasion.” Whether the shrub invasion was caused by an actual establishment of new plants or by increased height growth of plants already in place is not known. Most likely it was a combination of both.

It is unfortunate that the descriptions of the interlevee basin vegetation of 1966 are not accompanied by quantitative data because the community types described for this habitat in the Eyak River Marsh seem to agree quite well with what was present there immediately after the earthquake. This vegetation seems to have changed very little.

Similarly, narrative descriptions of the *Carex lyngbyaei* vegetation in the tidal zone at the base of the levees in 1966 indicate that this vegetation was similar to that of the tidal meadow of the Eyak River Marsh. However, the Eyak River Marsh is the only location within the western Copper River Delta where an extensive tidal meadow has developed seaward of the foreshore levee. A narrow band of *C. lyngbyaei* meadow is present for many kilometer along the base of the foreshore levee east of the Eyak River, but this meadow rarely exceeds 100 meters in width compared to the more than 1.2-kilometer width of the meadow at the Eyak River Marsh. A narrow zone of scattered patches, rings, and tussocks of sedge is very poorly developed seaward of the narrow sedge meadow strip. The reason for the minimal development is obscure. One factor may be a much steeper slope gradient on the tidal flats as compared to the Eyak River Marsh. This cannot be verified in the absence of a precise leveling survey; however, waterfalls over 2 meters high are present in the channels of small creeks that cross the tide flat, indicating a relatively steep slope gradient. Well-defined bordering levees do not seem to be present along the creeks extending into the more eastern tideflats. As these are where the initial colonization by the sedge takes place, levee development is prerequisite to marsh formation.

Conclusions

Perhaps the feature of the present wetland vegetation that is most changed since the 1964 earthquake is the deterioration of the sharp ecotones between the vegetation zones. The picture that emerges from the available preearthquake information is that of a diverse wet shrubland on the interior wetlands with an abrupt change to a wet prairie 5 to 6 kilometers inland from the tidal flats. Once beyond the shrubline, an observer was immediately confronted with vast open vistas that seemed to go forever. That this area was only a few kilometers wide in a north-south direction could not be distinguished because the terrain was almost flat and the horizon was either the ocean or hidden in clouds and mist. To the east, the closest mountain range was over 60 kilometers away, which further emphasized the vastness.

The wet shrubland-wet prairie ecotone still exists today, but it is not as well defined and the extremely long uninterrupted vistas are gone. The views now are across only a few hundred meters of interlevee basin to dense groves of shrubs surrounding the basin in all directions. The mountain ranges to the east or west are still visible by looking upward, but only from the new marshes at the mouth of the Eyak River is a long view possible.

The extension of shrubs into the open marshland zone appears to have been taken negatively, not only by the local population, but by some resource managers and scientists as well (USDA Forest Service 1981). A change from an herbaceous vegetation to one dominated by shrubs is the normal and natural pattern of successional on tidal marshes. It already was taking place on the Copper River Delta wetlands before the earthquake uplift, but at a very low rate. In vegetation, there is, of course only succession. A stable vegetation is one where the rate of succession is low but nevertheless is taking place. Succession occurs in response to the nature and combination of intrinsic and extrinsic environmental influences as controlled by the genetic potential of the component taxa. When these proceed or fluctuate at low levels, the vegetation responds accordingly. When a high rate of environmental change occurs (for example, a 2-meter tectonic uplift), the rate of succession increases and major changes in taxa composition, structure, and distribution can be seen in a relatively short time. For some reason, this natural phenomenon is disturbing to many humans.

Because of the geographic location between land and sea, tidal marshes have a highly dynamic vegetation. The process of reciprocal positive ecological feedback between plant and environment may be more evident in tidal marshes than in most other types of vegetation. On a small scale, the basically geological process of levee development is enhanced by the establishment of herbaceous vegetation, which, in turn, increases the rate of sediment accretion such that depositional rates decrease—this because the substrate surface becomes higher than the level of the tide. This has taken place on the Eyak River Marsh at a relatively rapid rate and continues to do so. Well-developed tidal meadows were present within 10 years after the 1964 uplift on the more landward portion of old, barren tidal flats where fishermen set their gillnets for salmon.

After five more years, this marsh extended seaward for more that a kilometer, and the upper part of the tidal marsh was changing from herbaceous meadow to shrubland. Similar changes in the physiognomy and composition of the vegetation were taking place on the marshlands present before the earthquake. These successional developments continue—some, such as the seaward extension of sedge meadow or the spread of shrubs onto levees, at slower rates; others, such as the increase of shrub cover on the least tidal portion of the new marsh, at faster rates—at least for a while.

It is difficult to determine what the rates of succession would have been had the uplift not occurred, because the entire delta area was uplifted, which left no control in the scientific sense. From the minimal information available on the preearthquake vegetation (Trainer 1959) and on the immediate postearthquake vegetation (Crow 1968), it is evident that woody species were not absent from the outer marshes. Both *Myrica gale* and a prostrate species of willow (*Salix arctica; S. reticulata*) were present in 1959, and a *Myrica/Festuca* C-T on slightly more inland levees was present in 1966. Small inclusions of *M. gale* were present in 1966 in the *Deschampsia-Potentilla* C-T, and this herbaceous community type possibly is a precursor of the *Myrica/Festuca* C-T. Given the ability of *M. gale* to fix atmospheric nitrogen, it is possible species of willow could establish and grow in the *Myrica/Festuca* C-T. *Salix* spp., *M. gale*, and *Alnus crispa* all grow sympatrically on the foreshore levee of the Eyak River Marsh. *Picea sitchensis* and *Populus trichocarpa* are present at low abundance in some stands, and further successional development to a mixed forest vegetation is possible. The presence of two buried *Picea sitchensis* forests beneath the marsh has been mentioned.

But what of the future? The Copper River Delta is in one of the most active tectonic zones on the surface of Earth. When—not if—the next earthquake occurs in that area, the Copper River Delta cannot avoid being affected. What happens to the vegetation when another uplift occurs? Probably more of the same.

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Appendix 1

In the following list, a double asterisk (**) preceding the scientific name indicates that the species was used directly as an attribute in the SIMID-CLUST analysis to determine the vegetation types; a single asterisk (*) indicates that the species was combined into the appropriate "other" class. Species without asterisks are those found on the 4- by 20-meter sample stands but not on any of the 20 0.1-centare quadrats. Nomenclature for vegetation follows Hulten (1968).

Woody plants:

** *Alnus crispa* (Ait.) Pursh ssp. *sinuata*

* *Menziesia ferruginea* Sm.

** *Myrica gale* L. var. *tomentosa* C. DC.

* *Picea sitchensis* (Bong.) Carr.

* *Populus balsamifera* L. spp. *trichocarpa* (Torr. & Gray) Hult.

Salix alaxensis (Anderss.) Cov.

** *Salix arctica* Pall. ssp. *crassijulius* (Traultv.) Skvortz.

** *Salix barclayi* Anderss.

* *Salix commutata* Bebb

Salix ovalifolia Traitv.

* *Salix reticulata* L. ssp. *orbicularis* (Anderss.) Flod.

* *Salix sitchensis* Sanson

Salix stolonifera Cov.

Sambucus racemosa L. ssp. *pubens* (Michx.) House var. *anborescens* Gray

* *Spiraea beauverdiana* Rydd.

* *Vaccinium uliginosum* L. ssp. *alpinum* (Bigel.) Hult.

Sedges:

* *Carex aquatilis* Wahlenb. ssp. *aquatilis*.

* *Carex laeviculmis* Meinsh.

* *Carex lyngbyaei* Hornem.

* *Carex pluriflora* Hult.

* *Carex ramenskii* Kom.

Grasses:

* *Agrostis alaskana* Hult.

** *Agrostis exarata* Trin.

* *Arctagrostis latifolia* (R.Br.) Griseb var. *arundinacea* (Trin.) Griseb.

* *Arctophila fulva* (Trin.) Anderss.

* *Calamagrostis canadensis* (Michx.) Beauv. ssp. *langsdorffii* (Link) Hult.

Calamagrostis deschampsioides Trin.

** *Deschampsia beringensis* Hult.

** *Festuca rubra* L. ssp. *aucta* (Krecz. & Bohr.) Hult.

* *Hierochloe odorata* L. (Wahlenb.)

* *Hordeum brachyantherum* Nevski

* *Poa eminens* Presl.

* *Puccinellia nutkaensis* (Presl) Fem. & Weath.

* *Puccinellia phryganodes* (Trin.) Scribn. & Merr.

Forbs:

* *Achillea borealis* Bong.

* *Actaea rubra* (Ait.) Willd. ssp. *arguta* (Nutt.) Hult.

* *Angelica lucida* L.

* *Angelica genuflexa Nutt.*

Artemisia tilesii Ledeb. ssp. *elatior* (Torry & Gray) Hult.

* *Athyrium filix-femina* (L.) Roth ssp. *cyclosorum* (Rupr.) Christens.

* *Caltha palustris* L. ssp. *assarifolia* (DC.) Hult.

* *Caltha leptoselpala* DC.

* *Chrysanthemum arcticum* L. ssp. *arcticum*

** *Cicuta douglassii* (DC.) Coult. & Rose.

* *Cicuta mackenzieana* Raup.

* *Conioselinum chinense* (t.) BSP.

* *Dodecatheon pulchellum* (Raf.) Merr. ssp. *superbum* (Pennell & Stair) Hult.

Eleocharis acicularis (L.) Roem. & Schult.

* *Eleocharis kamtschatica* (C.A- Mey.) Kom.

* *Eleocharis palustris* (L.) Roem. & Schult.

* *Epilobium angustifolium* L. ssp. *macrophyllum* (Haussk.) Hult.

* *Epilobium glandulosum* Lehm.

** *Epilobium hornemannii* Rchb.

** *Equisetum arvense* L.

* *Equisetum fluviatile* L. ampl. Ehrh.

* *Equisetum pratense* L.

* *Eriophorum angustifolium* Honck. ssp. *scabriusculum* Hult.

* *Eriophorum russeolum* E. Fries var. *majus* Sommier.

* *Euphrasia mollis* (Ledeb.) Wettst.

Fritillaria camschatcensis (L.) Ker-Gawl.

** *Galium trifidum* L. ssp. *columbianum* (Rydb.) Hult.

* *Galium triflorum* Michx.

Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch.

* *Heracleum lanatum* Michx.

* *Heuchera glabra* Willd.

* *Hippuris tetraphylla* L. f.

* *Hippuris vulgaris* L.

** *Iris setosa* Pall. ssp. *setosa*

* *Juncus alpinus* Vill. (in broad sense)

** *Juncus arcticus* ssp. *sitchensis* Engelm.

** *Lathyrus palustris* L. ssp *pilosus* (Cham.) Hult.

Ligusticum scoticum L. ssp. *hultenii* (Fem.) Calder & Taylor

* *Lomatogonium rotatum* (L.) E. Fries.

Lupinus nootkatensis Donn.

* *Lysimachia thyrsiflora* L.

Malaxais monophylla (L.) Sw.

* *Menyanthes trifoliata* L.

* *Mimulus guttatus* DC.

* *Myriopbyllum spicatum* L.

* *Nuphar polysepalum* Engelm.

* *Parnassis palustris* L. ssp. *neogaea* (Fem.) Hult.

* *Pedicularis paryiflora* J. F. Sm. ssp. *paryiflora*.

* *Plantago macrocarpa* Chain. & Schlecht.

* *Plantago martima* L. ssp. *juncoides* (Lam.) Hult.

* *Platanthera dilatata* (Pursh) Lindl.

* *Polygonum viviparum* L.

** *Potentilla egedii* Wormsk. ssp. *grandis* (Torr. & Gray) Hult.

Potentilla palustris (L.) Scop.

* *Potamogeton* sp. L.

Prenanthes alata (Hock.) Dietr.

* *Primula egaliksensis* Wormsk.

* *Pyrola assarifolia* Michx. var. *purpurea* (Bunge) Fern.

* *Ranunculus cymbalaria* Pursh.

Ranunculus hyperboreus Rottb. ssp. *hyperboreus*.

* *Rhinanthus minor* L. ssp. *borealis* (Sterneck) Love.

* *Rorippa islandica* (Oeder) Borb.
* *Rumex fenestratus* Greene
* *Rumex transitorius* Rech. f.
* *Sanguisorba stipulata* Raf.
* *Sparganium angustifolium* Michx.
* *Spiranthes romanzoffiana* Cham.
* *Stellaria humifusa* Rottb.
* *Stellaria sitchana* Steud. ssp. *sitchana*
* *Trientalis europaea* L. ssp. *arctica* (Fisch.) Hult.
* *Triglochin maritimum* L.
* *Triglochin palustris* L.
* *Viola epipsila* Ledeb. ssp. *repens* (Turcz.) Becker.

Appendix 2

This list of animals includes those mentioned in the text. All are either resident in the Copper River Delta wetlands or commonly seen from May to October. Many other species are present either as breeders or migrants.

Birds (American Ornithologists' Union 1983):

Asio flammeus (Pontoppidan)	Short-eared owl
Branta canadensis (Linnaeus)	Canada goose
Circus syaneus (Linnaeus)	Marsh hawk
Gallinago gallinago (Linnaeus)	Common snipe
Haliaeetus lencocephalus (Linnaeus)	Bald eagle
Larus canus Linnaeus	Mew gull
Larus glaucescens Naumann	Glaucous-winged gull
Cygnus buccinator Richardson	Trumpeter swan
Phalaropus lobatus (Linnaeus)	Red-necked phalarope
Selasphorus rufus (Gmelin)	Rufous hummingbird
Sterna aleutica Baird	Aleutian tern
Sterna pontoppidan	Arctic tern

Mammals (Banfield 1974):

Alces alces gigas Miller 1899	Alaska moose
Canis latrans incolatus Hall 1934	Coyote
Canis lupus columbianus Goldman 1941	Wolf
Castor canadensis belugae Bang 1913	Beaver
Ursus arctos Linnaeus	Brown bear
Vulpes vulpes alascensis Merriam 1900	Red fox

Fish (McPhail and Lindsey 1970):

Gasterosteus aculetus Linnaeus	Threespine stickleback
Oncorhychus kisutch (Walbaum)	Silver salmon

Amphibian (Pratt 1935):

Bufo boreas boreas Baird and Girard	Northwestern toad

Appendix 3

Table 5—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the tidal low marsh, *Carex* C-T, 1983 and 1979

	1983			1979		
	Percent coverage			Percent coverage		
Composition	$\bar{x}$	se	Percent constancy	$\bar{x}$	se	Percent constancy
Woody taxa: absent						
Graminoid taxa:						
Carex lyngbyaei	63.3	9.4	100	45.7	9.5	100
Calamagrostis canadensis	.4	.4	8			
Festuca rubra				T		
Deschampsia beringensis	T[a]		8	T		8
Agrostis exerata						
Other graminoid taxa	1.3	1.1	54	1.8	1.1	69
Total graminoid taxa	65.0			47.5		
Forb taxa:						
Potentilla egedii	2.0	1.1	38	1.8	1.0	31
Cicuta douglasii	T		8		*b*	15
Equisetum arvense						
Lathyrus palustris	T		8			
Athyruim filix-femina						
Eplobium hornemannii						
Galium trifidum						
Iris setosa						
Juncus arctius	T		8			
Erpilobium angustifolium						
Other forb taxa	3.0	2.2	85	3.2	2.2	85
Total forb taxa	5.0			5.1		
Total vascular plants	74.7			50.7		
Cryptogamic taxa	8.6	7.6	54	8.2	7.1	31
Total live vegetation	83.3			58.9		
Attached dead and litter	4.8	1.9	69	24.0	7.2	92
Total vegetation coverage	88.1			82.9		
Bare substrate	72.1	9.6	85	63.0	8.5	92
Surface water	33.0	10.7	69	18.4	7.7	69

[a] T = less than 0.1 percent canopy coverage.
[b] Standard errors not calculated when canopy coverage ≤ 0.1.

Table 6—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the tidal high marsh, *Carex* C-T, 1983 and 1979

	1983			1979		
	Percent coverage			Percent coverage		
Composition	$\bar{x}$	se	Percent constancy	$\bar{x}$	se	Percent constancy
Woody taxa:						
Myrica gale	0.8	0.8	25	0.3	0.3	13
Salix barclayi	T[a]		13	T		13
Alnus crispa						
Salix arctica	.1		13			
Other woody taxa	.1		13			
Total woody taxa	1.0			.3		
Graminoid taxa:						
Carex lyngbyaei	80.9	5.0	100	61.7	6.7	100
Calamagrostis canadensis	.6		13	T		13
Festuca rubra	.2		13			
Deschampsia beringensiss	T		50	1.3	.5	63
Agrostis exerata	T		25			
Other graminoid taxa	.1		75	T		38
Total graminoid taxa	82.0			69.1		
Forb taxa:						
Potentilla egedii	1.3	.7	88	1.5	.8	63
Cicuta douglasii	.2	.1	50	T		38
Equisetum arvense						
Lathyrus palustris						
Athyrium filix-femina						
Epilobium hornemannii	.2	.1	38	.3	.2	63
Galium trifidum	.3	.2	63	T		25
Iris setosa						
Juncus arctius	.1		100	.9	.4	63
Epilobium angustifolium						
Other forb taxa	3.6	.5	100	3.9	1.1	100
Total forb taxa	5.7			6.6		
Total vascular plants	88.6			74.6		
Cryptogamic taxa	6.1	2.4	100	.8	.3	75
total live vegetation	94.7			75.4		
Attached dead and litter	79.9	6.7	100	61.0	5.5	100
Total vegetation coverage	174.6			136.4		
Bare substrate	11.5	5.6	88	32.6	5.7	100
Surface water	28.7	6.8	100	24.3	6.0	88

[a] T = less than 0.1 percent canopy coverage.

Table 7—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the tidal low levee, *Carex/Potentilla* C-T, 1983 and 1979

Composition	1983 Percent coverage $\bar{x}$	1983 Percent coverage se	1983 Percent constancy	1979 Percent coverage $\bar{x}$	1979 Percent coverage se	1979 Percent constancy
Woody taxa:						
Myrica gale	5.8	3.9	43	0.8	0.5	43
Salix barclayi	.1	[a]	29	T[b]		14
Alnus crispa	T		14			
Salix arctica	0.5	.4	29			
Other woody taxa	T		14			
Total woody taxa	6.4				.8	
Graminoid taxa:						
Carex lynbyaei	54.6	10.8	100	63.6	9.9	100
Calamagrostis canadensis				T		14
Festuca rubra	2.4	1.6	57	.2	.2	43
Deschampsia beringensis	.9	.6	71	2.8	1.1	86
Agrostis exerata	T		29	T		14
Other graminoid taxa	.1		43	.4	.1	86
Total graminoid taxa	58.0			67.1		
Forb taxa:						
Potentilla egedii	22.1	3.1	100	13.5	3.3	100
Cicuta douglasii	T		14	T		14
Equisetum arvense	.9	.8	43	T		14
Lathyrus palustris	T		14			
Athyrium filix-femina						
Epilobium hornemannii	T		14	T		57
Galium trifidum	T		29	T		43
Iris setosa	T		29			
Juncus arctius	.8	.6	57	.4	.3	29
Epilobium angustifilium						
Other forb taxa	3.2	.7	100	4.3	1.6	100
Total forb taxa	27.1			18.5		
Total vascular plants	91.5			86.4		
Cryptogamic taxa	9.1	4.4	71	7.0	4.3	71
Total live vegetation	100.6			93.4		
Attached dead and litter	60.5	8.3	100	54.1	10.6	100
Total vegetation coverage	161.1		147.5			
Bare substrate	28.8	5.2	100	40.1	10.8	86
Surface water	11.6	7.7	43	13.2	8.7	29

[a] Standard errors not calculated when canopy coverage is ≤ 1.

[b] T = Less than 0.1 percent canopy coverage.

Table 8—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the tidal high levee, *Myrica/Carex* C-T, 1983 and 1979

	1983			1979		
	Percent coverage		Percent	Percent coverage		Percent
Composition	$\bar{x}$	se	constancy	$\bar{x}$	se	constancy
Woody taxa:						
Myrica gale	87.2	[a]		3.6		
Salix barclayi	.2			.9		
Alnus crispa						
Salix arctica	.4			.2		
Other woody taxa	8.9					
Total woody taxa	96.7			4.7		
Graminoid taxa:						
Carex lyngbyaei	23.0			32.1		
Calamagrostis canadensis	1.1			.2		
Festuca rubra	3.8			2.1		
Deschampsia beringensis	.3			2.2		
Agrostis exerata	1.0					
Other graminoid taxa						
Total graminoid taxa	29.2			36.6		
Forb taxa:						
Potentilla egedii	8.4					
Cicuta douglasii	.2					
Equisetum arvense						
Lathyrus palustris						
Athyrium filix-femina						
Epilobium hornemannii				.2		
Galium trifidum	.1			.1		
Iris setosa	.1					
Juncus arcticus	2.0			4.4		
Epilobium angustifolium						
Other forb taxa	.8			6.5		
Total forb taxa	11.6			17.0		
Total vascular plants	137.5			58.3		
Cryptogamic taxa	6.1			36.2		
Total live vegetation	143.6			94.5		
Attached dead and litter	100.0			81.7		
Total vegetation coverage	243.6			176.2		
Bare substrate						
Surface water	1.0			11.4		

[a] Only 1 stand included, standard errors cannot be calculated.

Table 9—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the nontidal foreshore levee, *Alnus/Myrica-Salix//Equisetum* C-T, 1983 and 1979

Composition	1983 Percent coverage $\bar{x}$	1983 Percent coverage se	1983 Percent constancy	1979 Percent coverage $\bar{x}$	1979 Percent coverage se	1979 Percent constancy
Woody taxa:						
Myrica gale	44.9	11.4	100	13.6	2.9	100
Salix barclayi	20.1	6.1	100	7.8	4.2	100
Alnus crispa	21.5	9.3	100	1.7	1.3	75
Salix arctica	T[a]		25	T		25
Other woody taxa	6.1	3.1	75	3.0	1.1	100
Total woody taxa	92.6			26.0		
Graminoid taxa:						
Carex lyngbyaei	23.3	6.9	100	30.4	7.1	100
Calamagrostis canadensis	7.3	2.9	100	4.3	1.8	100
Festuca rubra	1.1	.4	75	3.1	.5	100
Deschampsia beringensis	T		25	.2	.2	50
Agrostis exerata	.6	.3	100	.5	.5	50
Other graminoid taxa	.1		25	.4	.3	75
Total graminoid taxa	32.3			38.9		
Forb taxa:						
Potentilla egedii	2.2	1.0	100	9.1	2.9	100
Cicuta douglasii	1.4	.8	75	1.9	.9	75
Equisetum arvense	32.7	10.4	100	9.9	4.4	100
Lathyrus palustris	.9	.9	75	.7	.6	50
Athyrium filix-femina	4.6	3.7	75	.5	.2	75
Epilobium hornemannii	.3	.1	100	2.5	.8	100
Galium trifidum	.6	.2	100	.7	.2	100
Iris setosa	.1		50	T		50
Juncus arcticus	.9	.8	50	1.0	.9	100
Epilobium angustifolium	T		25			
Other forb taxa	4.4	.7	100	5.1	2.3	100
Total forb taxa	48.1			31.3		
Total vascular plants	172.9			96.2		
Cryptogamic taxa	55.8	11.8	100	7.6	7.6	25
Total live vegetation	228.7			103.8		
Attached dead and litter	64.3	10.2	100	21.8	8.7	100
Total vegetation coverage	293.0			125.6		
Bare substrate				0.4	.2	75
Surface water	1.8	1.7	50	2.6	2.6	25

[a] T = less than 0.1 percent canopy coverage.

Table 10—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the foreshore levee, *Myrica/Carex-Calamagrostis* C-T, 1983 and 1979

	1983			1979		
	Percent coverage		Percent constancy	Percent coverage		Percent constancy
Composition	$\bar{x}$	se		$\bar{x}$	se	
Woody taxa:						
Myrica gale	49.1	21.1	100	35.5	15.3	100
Salix barclayi	9.4	2.9	100	1.7	.9	67
Alnus crispa	2.0	1.5	100	10.7	7.4	67
Salix arctica						
Other woody taxa	.1	[a]	67			
Total woody taxa	60.7			48.0		
Graminoid taxa:						
Carex lyngbyaei	32.8	8.1	100	32.0	10.7	100
Calamagrostis canadensis	27.0	8.8	100	19.9	13.7	100
Festuca rubra	9.8	4.5	100	.9	.5	100
Deschampsia beringensis	.2	.2	33	1.4	1.0	67
Agrostis ecerata	.4	.3	33	1.1	1.1	33
Other graminoid taxa	.3	.3	33	.1		67
Total graminoid taxa	70.3			55.5		
Forb taxa:						
Potentilla egedii	.4	.2	100	1.6	1.1	67
Cicuta douglasii	.5	.3	100			
Equisetum arvense	5.2	4.3	100	8.8	8.8	33
Lathyrus palustris	1.8	1.8	33	0.6	0.6	33
Athyrium filix-femina	T[b]		33	2.1	2.1	67
Eqilobium hornemannii	2.2	0.8	100	2.2	0.8	100
Galium trifidum	1.6	0.8	100	T		67
Iris setosa	T		33			
Juncus arcticus	0.1		33	1.4	1.4	33
Epilobium angustifolium						
Other forb taxa	1.5	0.8	100	1.2	0.8	100
Total forb taxa	13.2			18.0		
Total vascular plants	144.1		121.5			
Cryptogamic taxa	27.3	13.4	100	30.3	14.8	100
Total live vegetation	171.4		151.8			
Attached dead and litter	97.6	2.4	100	62.5	9.8	100
Total vegetation coverage	269.0		214.3			
Bare substrate				T		33
Surface water	0.4	0.3	67	9.4	5.7	67

[a] Standard errors not calculated when canopy coverage is ≤ 0.1.

[b] T= Less than 0.1 percent canopy coverage.

Table 11—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the interior levee, *Carex/Equisetum-Lathyrus* C-T, 1983 and 1979

	1983			1979		
	Percent coverage			Percent coverage		
Composition	$\bar{x}$	se	Percent constancy	$\bar{x}$	se	Percent constancy
Woody taxa:						
Myrica gale	4.9	1.7	75	5.3	3.8	58
Salix barclayi	.7	.3	58	1.6	.7	67
Alnus crispa	2.2	1.7	50	4.1	4.0	17
Salix arctica	1.2	.6	67	2.6	1.3	42
Other woody taxa	2.5	1.6	58	.9	.4	75
Total woody taxa	11.6			14.5		
Graminoid taxa:						
Carex lyngbyaei	53.0	2.7	100	20.7	3.5	100
Calamagrostis canadensis	1.8	1.0	58	4.8	3.0	83
Festuca rubra	6.5	1.6	100	13.3	2.5	100
Deschampsia beringensis	4.1	1.1	100	14.1	4.6	100
Agrostis exerata	.4	.2	75	.4	.3	42
Other graminoid taxa	3.0	1.2	92	4.0	1.5	92
Total graminoid taxa	68.8			57.3		
Forb taxa:						
Potentilla egedii	7.7	4.0	100	11.4	2.2	100
Cicuta douglasii	1.3	.6	75	1.6	.7	83
Equisetum arvense	30.2	4.5	100	10.8	3.1	100
Lathyrus palustris	21.0	4.3	92	5.1	1.0	92
Athyrium filix!-femina	6.9	1.6	92	5.3	1.6	100
Evilobium hornemannii	2.7	.4	100	13.4	3.1	100
Galium trifidum	2.1	.5	92	2.9	1.0	83
Iris setosa	3.3	1.0	92	1.0	.4	75
Juncus arcticus	T[a]	[b]	17			
Epilobium angustifolium	1.6	.9	33	.1		33
Other forb taxa	5.3	1.4	100	9.5	1.8	100
Total forb taxa	82.1			61.1		
Total vascular plants	162.4			133.9		
Cryptogamic taxa	69.1	5.1	100	25.4	2.6	100
Total live vegetation	232.0			161.3		
Attached dead and litter	65.0	4.5	100	45.1	5.7	100
Total vegetation coverage	297.0			203.6		
Bare substrate	T		8	.9	.4	50
Surface water	.2	.2	8			

[a] T = less than 0.1 percent canopy coverage.

[b] Standard errors not calculated when canopy coverage is ≥ 0.1.

Table 12—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the moderately hydric interlevee basin, *Carex/Lathyrus* C-T, 1983 and 1979

Composition	1983 Percent coverage x̄	1983 Percent coverage se	1983 Percent constancy	1979 Percent coverage x̄	1979 Percent coverage se	1979 Percent constancy
Woody taxa:						
Myrica gale	1.8	1.8	14	1.2	0.8	29
Salix barclayi				T[a]	[b]	14
Alnus crispa	.6	.6	14			
Salix arctica						
Other woody taxa	.2	.2	29	.8	.8	100
Total woody taxa	2.5			2.0	.8	
Graminoid taxa:						
Carex lyngbyaei	78.8	7.2	100	63.7	12.4	100
Calamagrostis canadensis	6.6	3.8	57	2.4	1.3	43
Festuca rubra	4.8	1.1	100	15.7	5.0	100
Deschampsia beringensis	1.1	.4	100	5.6	2.3	71
Agrostis exerata	1.2	.6	71	.3	.2	43
Other graminoid taxa	.3	.2	71	.4	.2	57
Total graminoid taxa	92.7			88.2		
Forb taxa:						
Potentilla egedii	4.2	3.2	86	4.5	2.6	71
Cicuta douglasii	.7	.2	86	.6	.3	86
Equisetum arvense	10.5	7.0	43	3.0	1.9	43
Lathyrus palustris	12.3	2.7	100	12.9	4.2	100
Athyrium filix-femina	4.3	2.6	43	2.2	1.4	29
Epilobium hornemannii	2.3	.7	100	5.0	3.2	100
Galium trifidum	2.7	.6	100	3.0	1.0	100
Iris setosa	T		14	2.0	2.0	29
Juncus arcticus	T		14			
Epilobium angustifolium	2.1	2.1	14	T		14
Other forb taxa	1.3	.6	86	4.5	2.1	570
Total forb taxa	40.4			37.8		
Total vascular plants	135.6		128.0			
Cryptogamic taxa	45.1	9.3	100	15.5	7.4	86
Total live vegetation	180.7			143.5		
Attached dead and litter	74.9	6.4	100	72.4	12.4	100
Total vegetation coverage	255.6		215.9			
Bare substrate				.2	.2	14
Surface water	.6	.6	14	3.5	3.0	29

[a] T = Less than 0.1 percent canopy coverage.

[b] standard errors not calculated when canopy coverage is ≤ 0.1.

Table 13—Characteristic taxa composition, mean percentage canopy coverage, and percentage constancy in the hydric interlevee basin, *Cicuta/Carex-Festuca* C-T, 1983 and 1979.

Composition	1983 Percent coverage $\bar{x}$	1983 Percent coverage se	1983 Percent constancy	1979 Percent coverage $\bar{x}$	1979 Percent coverage se	1979 Percent constancy
Woody taxa:						
Myrica gale				1.3	1.3	13
Salix barclayi				1.4	1.4	25
Alnus crispa	0.1	0.1	25	2.7	1.8	25
Salix arctica	T[a]	[b]	25			
Other woody taxa	.6	.6	38	1.9	1.9	25
Total woody taxa	.7			7.3		
Graminoid taxa:						
Carex lyngbyaei	74.1	9.4	100	64.7	8.8	100
Calamagrostis canadensis	1.8	1.6	38	1.6	1.0	38
Festuca rubra	8.2	2.8	100	16.4	4.8	88
Deschampsia beringensis	4.0	1.5	75	6.6	2.4	88
Agrostis exerata	.4	.2	38			
Other graminoid taxa	1.0	.4	50	2.4	.9	75
Total graminoid taxa	89.5			91.6		
Forb taxa:						
Potentilla egedii	.8	.5	38	.9	.5	38
Cicuta douglasii	12.6	3.0	100	27.6	9.8	100
Equisetum arvense	2.1	1.3	50	.6	.5	25
Lathyrus palustris	9.0	1.7	88	22.1	7.1	88
Athyrium filix-femina	T		13	.3	.1	38
Epilobium hornemannii	1.9	1.2	62	.9	.3	88
Galium trifidum	.9	.7	25	1.5	.9	53
Iris setosa	T		13			
Juncus arcticus						
Epilobium angustifolium						
Other forb taxa	2.9	1.6	62	1.1	.7	50
Total forb taxa	30.2			55.0		
Total vascular plants	120.5		153.9			
Cryptogamic taxa	59.0	12.0	100	17.3	7.5	88
Total live vegetation	179.5		171.2			
Attached dead and litter	61.6	9.2	100	74.1	10.5	100
Total vegetation coverage	241.0		245.3			
Bare substrate				.1	.1	13
Surface water	.7	.7	13	6.5	6.5	13

[a] T = less than 0.1 percent canopy coverage.

[b] Standard errors not calculated when canopy coverage is ≤ 0.1.

Table 14—Substrate features of new marshland community types

	Community types							
	Carex C-T, low marsh (13 stands)		*Carex* C-T, high marsh (8 stands)		*Carex/Potentilla* C-T, low levee (7 stands)		*Myrica/Carex* C-T, high levee (1 stand)	
Substrate component	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Thickness of organic layer (centimeters)	0.5	0.2	2.1	0-3	2.6	0-3	4.0	1.4
Rooting depth (centimeters)	22.1	1.4	22.3	0-5	22.9	0-5	21.0	0.0
Depth to water table (centimeters)	15.6	1.2	7.8	1-3	18.9	1.0	5.0	4.2
Salinity (‰)	5.3	1.0	2.3	0.8	3.3	1.8	0.2	0.1
Conductivity (millimohs per square centimeter)	634	87	254	49	384	19	87	7
Reaction (pH)	6.4	0.1	5.8	0.1	5.7	0.1	5.1	0.1
Texture (percent of cores):								
Sand	69		26		14			
Sandy silt			13		29			
Silt	31		63		51		100	

Table 15—Substrate features of the old marshland community types

	Community types									
	Alnus/Myrica Salix/Equisetum foreshore levee (4 stands)		*Myrica/Carex, Calamagrostis* C-T, foreshore levee (3 stands)		*Carex/Equisetum Lathyrus* C-T, interior levee (12 stands)		*Carex-Lathyrus* C-T, interlevee basin (7 stands)		*Cicuta/Carex Festuca* C-T, interlevee basin (8 stands)	
Substrate component	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Thickness of organic layer (centimeters)	9.1	1.8	14.7	3-0	14.7	1.0	22.1	1-7	24.4	1.2
Rooting depth (centimeters)	30.0	0.0	26,6	2.0	30.0	0.0	30.0	0.0	30.0	0.0
Depth to water table (centimeters)	21.1	2-7	10.2	1-7	16.3	0.6	18.1	1-9	20.7	0.0
Salinity (‰)	0	0	0	0	0	0	0	0	0	0
Conductivity (millimohs per square centimeter)	306	19	284	68	331	11	368	18	361	15
Reaction (pH)	5.8	0.1	5.1	0-3	5.6	0.1	5.5	0.1	5.7	0.1
Texture (percentage of cores):										
Sand			33							
Sandy silt			33				29		13	
Silt	100		33		100		71		87	

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The Copper River Delta stretches more than 75 kilometers along the south-central coast of Alaska. It is the terminus of the outwash deposits from a large part of the most heavily glaciated region of North America, and all major rivers that Row into the delta carry extremely high levels of suspended sediments. Wetlands extended inland for as much as 20 kilometers. In 1964, an earthquake of Richter scale 8.4 to 8.6 raised the entire delta from 1.6 to 3.4 meters above the previous mean sea level. This paper documents the changes in tidal areas and plant succession in those areas. The uplift appears to have altered locations and rates, but not the nature, of wetland plant succession on the delta.

Keywords: Copper River Delta, plant ecology, plant succession, tidal marshlands, tectonic uplift, Alaska.

Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, Oregon 97208-3890