WETLANDS, Vol. 19, No. 1, March 1999, pp. 13–27
© 1999, The Society of Wetland Scientists

RESPONSE OF MARINE DELTAIC SURFACES TO MAJOR EARTHQUAKE UPLIFTS IN SOUTHCENTRAL ALASKA

Keith Boggs and Michael Shephard[1]
Alaska Natural Heritage Program
University of Alaska Anchorage
Anchorage, Alaska, USA 99501

[1] *U.S. Forest Service*
Tongass National Forest
Sitka, Alaska, USA 99835

Abstract: Major earthquake uplifts in south-central Alaska of marine deltaic surfaces to an inter-tidal or supra-tidal status cause drastic shifts in processes and vegetation. To assess long-term ecosystem changes as a deltaic landscape converted from a tidal marsh to a supra-tidal wetland, we studied a four-stage chronosequence of deltaic surfaces (30-yr-old inter-tidal surface, 352-yr-old inter-tidal surface, 30-yr-old supra-tidal surface, and 280-yr-old supra-tidal surface). Plots were used to gather landform, soils, and vegetation information, and landform schematics and aerial photo interpretation were used to determine their spatial distribution. Succession progressed on inter-tidal surfaces from pioneer species (principally *Carex lyngbyaei*) on newly uplifted mud flats, to a mature tidal marsh with channels, levees, and basins dominated by *Carex lyngbyaei* with thick root mats. Uplift of the mature tidal surface to a supra-tidal status allowed freshwater tolerant species (*Equisetum fluviatile, Sphagnum* spp.) to invade the basins, and trees and shrubs displaced herbaceous vegetation on levees. On the oldest supra-tidal surface, basins developed peatlands (*Andromeda polifolia, Sphagnum* spp.), and pH decreased. Levees supported trees or shrubs on mineral or peat soils. Vegetation zonation within a basin-levee complex was evident and repeated, with some variation, across the surfaces. At the landscape scale moving inland, gradients in vegetation occurred on all surface ages.

Key Words: Alaska, *Carex lyngbyaei,* delta, earthquake, landform, landscape evolution, peatland, soils, *Sphagnum,* succession, tidal marsh, vegetation pattern

INTRODUCTION

Geologic uplift (tectonism) in south-central Alaska, along with the northern marine climate, has helped create a landscape of glacially carved mountains rising abruptly from the sea, supporting the largest icefields and valley glaciers in North America. Deposition of sediment from this region's silt-laden rivers has formed discontinuous piedmonts consisting of glacial outwash plains, coastal dunes, and tidal marshes formed at river mouths. Even with tectonic uplifts, interseismic periods between uplifts (ca. 280 to 780 yrs) are often long enough to allow for the development of mature tidal marshes (Plafker et al. 1990).

Examples of marine deltaic surfaces tectonically uplifted into or above the tidal influence are common along coastal Alaska (Crow 1968, Yehle 1975, Plafker et al. 1990, Thilenius 1990). Spatial and temporal relationships and processes controlling the distribution patterns of vegetation are drastically altered following these tectonic uplifts. Sub-tidal mud flats lifted to the inter-tidal zone are rapidly colonized by tide-tolerant vegetation, leading to the formation of levees and basins (Crow 1968, Thilenius 1995). When inter-tidal marshes are lifted to the supra-tidal zone, both the tides and accretion of marine deltaic sediments are lost from the system, and non-tidal vegetation invades (Crow 1968, Crow 1971, Potyondy et al. 1975, Batten et al. 1978, Campbell 1990, Thilenius 1990, Davidson and Klinge 1992, MacCracken 1992, Thilenius 1995, Stephenson 1995, Witten 1996, Boggs 1998).

The evolution of marine deltaic surfaces is of particular interest to land managers along the Gulf of Alaska. The Copper River Delta's tidal flats harbor the largest staging area for migratory shorebirds in North America. The delta is the sole nesting ground for the dusky Canada goose (*Branta canadensis occidentalis* [Baird]), whose population declined dramatically after a tectonic uplift in 1964 altered its nesting habitat (Crow 1971, Campbell 1990). Moose (*Alces alces* [Linnaeus]) habitat, in contrast, improved dramatically due to the uplift (MacCracken 1992, Stephenson

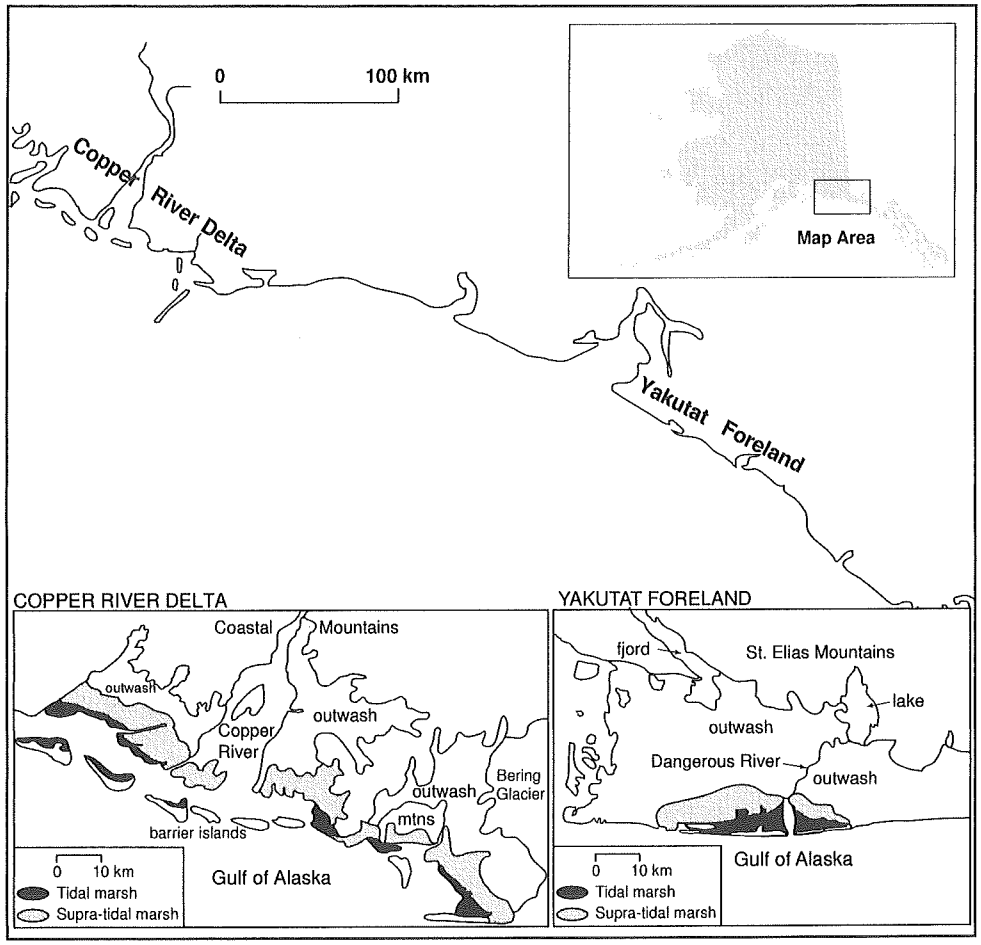

Figure 1. Location of tidal and supra-tidal marine deltaic landscapes on the Copper River Delta and Yakutat Forelands.

1995). These and other issues take on greater importance due to the rarity of tidal marshes within the region and the rapid vegetation and geomorphic changes resulting from subsidence or uplift of the landscape.

This paper describes the evolution of vegetation, landform, and soils as marine deltaic surfaces convert from tidal mud flat to tidal marsh to young supra-tidal surface and then to a mature supra-tidal surface. This four-stage chronosequence (Stevens and Walker 1970) spans approximately 600 yrs using surface descriptions from two similar regions, the Yakutat Foreland and the Copper River Delta, Alaska (see Study Area descriptions). Information for the second chronosequence stage (tidal marsh) is from a published description of the surface (Crow 1968), and the other three stages were sampled for this study. The chronosequence approach assumes that landscape evolution on all four surfaces shares a common trajectory, namely that the younger surfaces on the Copper River Delta in time will evolve into a mature deltaic surface similar to that found on the Yakutat Foreland. We develop a hypothesis for landscape evolution, address the persistence of some species and communities as relicts from previous tidal communities, and discuss viewing each surface age as a stage of landscape succession.

METHODS

Study Area

The three youngest surfaces occur on the Copper River Delta, and the oldest surface occurs on the Yakutat Foreland (Figure 1). The deltaic surfaces of both the Copper River Delta and Yakutat Foreland occur as part of broad low gradient (0–7%) piedmonts. These piedmonts are bordered by coastal mountains commonly 1,500 m in elevation, piedmont and valley glaciers, and seaward by the Gulf of Alaska. The deltas are thought to have some of the highest rates of sediment accumulation in the world (Molnia 1986). The Copper River alone transports 97,000,000 metric tons of sediment per year to the ocean and delta (Hampton et al. 1987).

This region has mild, wet summers and cool, wet

winters supporting wetlands, temperate rainforests, and alpine tundra. On the Copper River Delta, average yearly precipitation increases moving inland from 97 cm over open ocean to 218 cm mid-piedmont to 457+ cm at the mountain bases (Searby 1969). On the Yakutat Foreland, the average annual precipitation at a mid-piedmont weather station is 385 cm (National Climatic Data Center 1993). Mean monthly temperatures for both areas range from −3.8 °C in January to 12 °C in July.

Young Tidal Surface. The young tidal surface was sub- or inter-tidal prior to a 1964 tectonic uplift (moment magnitude = 9.2) that lifted the Copper River Delta from 1.8 to 3.4 m above the previous mean sea level (Reimnitz 1966). The uplift resulted in seaward shifts of the strandline as much as 4 km. This surface is now a prograding inter-tidal marsh (tidal surface) with marshes, mudflats, tide channels, and distributory channels (Batten et al. 1978, Thilenius 1990). It is bordered by the Gulf of Alaska and inland by the young supra-tidal deltaic surface described below (Figure 1). The vegetated portion of the surface is discontinuous, stretching 110 km parallel to the coastline (from latitude 60° 38′N to 60° 00′N and longitude 145° 52′W to 143° 30′W), with a maximum width of ca. 2 km on the surface's western edge.

Mature Tidal Surface. Physiognomic descriptions of the mature tidal surface are provided by Crow (1968), who described this surface immediately after it was uplifted to a supra-tidal status in 1964 (Figure 1, same area as that labeled "Supra-tidal marsh"). Even though Crow's vegetation descriptions are from a supra-tidal surface, they are interpreted here as that of a mature tidal surface because only limited physiognomic changes occurred during the 1- to 3-yr post-uplift period (Crow 1968). This is supported by transects Crow sampled between 1965 and 1967 extending from the levees to the basins to monitor changes in vegetation. Changes in species composition and physiognomy did occur during this period, but the overall character of the tidal marsh was maintained. Three new species invaded the *Carex lyngbyaei* dominated basins (20 to 23 species), and *Carex lyngbyaei* did not decrease in cover significantly, although changes in vigor and vitality were apparent. Three new species also invaded the ecotone between the *Hedysarum alpinum-Deschampsia beringensis* dominated levees and the basins (from 17 to 18 species, loss of 2 species). No new species invaded the *Hedysarum alpinum-Deschampsia beringensis* dominated levees. Further support for using Crow's results includes vegetation descriptions similar to those described by Trainer (1959) on the same surface prior to the uplift and to another mature tidal marsh of the region, the Stikine delta (del Moral and Watson 1978).

This surface was approximately 5 × 110 km long and was bordered seaward by the ocean and inland by glacial outwash plains or mountains (Figure 1). The surface was tidal with well-defined levees, basins, tide channels, distributory channels, and a wave cut sea cliff 1–2 m high fronting the marsh (Trainer 1959, Crow 1968). The basins were tidally-flooded on a daily basis, and extreme high spring tides (+4.2 m mean sea level) occasionally flooded the levees (Trainer 1959).

The landscape evolution of the Copper River Delta's mature tidal marsh was described by Plafker et al. (1990). A mature tidal marsh was tectonically lifted above the tidal influence 780 ± 115 yrs (C^{14} dating) prior to the 1964 uplift (given as 780 ± 115/— 1964 B.P.). Approximately 352 ± 148/— 1964 B.P., regional interseismic submergence (4.5–6.5 mm/yr) lowered the supra-tidal land surface into the inter-tidal zone, allowing development of a new tidal marsh on top of the supra-tidal marsh. The regional submergence did not lower the land surface into the sub-tidal zone because rates of accretion matched subsidence, as measured using varves (Plafker et al. 1990). Consequently, the mature tidal marsh was maintained until 1964, when it was uplifted again to the supra-tidal zone.

Young Supra-Tidal Surface. The young supra-tidal surface was the same surface described by Crow (1968), except it is now 30 yrs post 1964 uplift (Figure 1). The uplift raised the levees, basins, and most first and second order channels above extreme high tide. Most third+ order channels are still tidal, often incised due to post-earthquake down-cutting. This surface has maintained the landform pattern of the pre-1964 mature tidal marsh, with levees, basins, and channels occurring continuously across its width and length.

Mature Supra-Tidal Surface. The mature supra-tidal surface was a mature tidal marsh lifted above the tidal influence ca. 280 ± 80/— 1990 B.P. (Holloway 1990). This surface occurred on the Yakutat Foreland and was approximately 6 × 35 km (Figure 1; from latitude 59° 25′N to 59° 15′N and longitude 139° 30′W to 139° 00′W). It was bordered seaward by a narrow tidal surface and inland by outwash plains.

Radiocarbon C^{14} dates and soil pedon data from Holloway (1990) were used to provide a relative age for the surface. Tidal silt deposition and tidal marsh vegetation (predominantly *Carex* spp.) first appeared 1,090 ± 80/— 1990 B.P. Silt deposition ended at 430 ± 60/— 1990 B.P., and the marsh began to build peat; the species composition indicates a tidal peat. At 280 ± 80/— 1990 B.P., species typically found only in supra-tidal peatlands invaded the sites, indicating

abrupt acidification. These species included peat moss (*Sphagnum* spp.), the growth of which increased dramatically and began to close the open water, two diatom genera (*Eunotia* and *Pinnularia*) that typically occur only on acidic peatlands, and vascular and nonvascular species found only on supra-tidal peatlands. Vascular, nonvascular, and diatom species composition were relatively consistent over 280 years to the present as the peat increased in depth.

Landforms on the mature supra-tidal surface were similar to landforms of the young supra-tidal surface of the Copper River Delta and included levees, basins, and channels. First and second order channels were freshwater, and most third+ order channels were tidal and distributory. The tidal waters did not overtop the channel levees, which were approximately 3 m above mean sea level. Anthropogenic disturbance on all the deltaic surfaces was minimal.

Classification, Landform and Soils

On the three surfaces sampled for this study (young tidal, young supra-tidal, mature supra-tidal), interpretations of landforms from topographic maps (1:63,360) and aerial photography (true color and color infrared, 1:15,840) were used to separate marine deltaic surfaces from other adjacent landscapes, such as outwash plains. To sample fine-scale variability of vegetation-based community types, landform (channel, levee, and basin) and soils, an equal number of sample areas per surface were randomly selected from topographic maps using a grid and random numbers table. However, an unequal number of sample areas were sampled (13 on the young supra-tidal surface and eight on each of the young-tidal and mature supra-tidal surfaces) due to weather and logistics preventing us from reaching the areas (Steel and Torrie 1960, Mueller-Dombois and Ellenberg 1974). A single sample area consisted of a basin, levees bordering the basin, and the adjacent channels. Because no basins occurred on the young tidal surface, a sample area was a transect extending from unvegetated tidal mud flats, through the vegetated marsh, to the edge of the non-tidal zone. Weather and logistics also prevented us from sampling four of the randomly selected sample areas on the young supra-tidal surface. Similar areas that were accessible were substituted and sampled. Sampling occurred between late-June and early-September 1991–1994.

During reconnaissance of a sample area, a list of community types was compiled. A community type was considered to be somewhat homogeneous in all vegetation layers and differing from contiguous vegetation in quantitative and qualitative characteristics (Daubenmire 1968). Within a sample area on the young and mature supra-tidal surfaces, a single transect was randomly oriented to bisect the basin, extending across the levees and channels on both sites. These transects were used to ensure a degree of randomness in the placement of plots. Along each transect, one example of each community was selected without preconceived bias and then sampled (Mueller-Dombois and Ellenberg 1974). Communities occurring in the sample area but not found on the transect were also sampled.

One rectangular 50 m^2 (5 $\times$ 10 m) plot was placed in each community selected for sampling. A total of 132 plots were sampled: 30 in the young tidal surface, 72 in the young supra-tidal, and 30 in the mature supra-tidal. Percentage canopy cover was ocularly estimated for all vascular species per plot (Brown 1954, Daubenmire 1959). Nonvascular species with $>$ 5% cover were recorded, and total nonvascular cover was recorded. Plant specimens not identified in the field were collected and identified in the office or at the University of Alaska Fairbanks Herbarium. Vascular nomenclature follows Hulten (1968), and nonvascular follows Vitt et al. (1988).

Soils were described from one 80-cm-deep soil pit per plot in 107 of the plots: 28 in the young tidal surface, 49 in the young supra-tidal, and 30 in the mature supra-tidal. Using established methodology (USDA Soil Survey Staff 1975), the following variables were recorded: soil subgroup, depth to water table, horizon depth, structure, texture, and pH.

Schematic cross sections of physical site characteristics were constructed along each transect to evaluate changes in landform, water level, and soils. An Abney level and measuring stick were used to measure the elevation change in water level, mineral soil, and histic layer between the soil pits from each plot.

Vegetation-based community types were developed from a step-wise procedure of successive approximations using the plot data (Pfister and Arno 1980). Association tables of the preliminary dominance-type groupings were created using the species and cover data. Two-way indicator species analysis (Hill 1979), detrended correspondence analysis (Hill and Gauch 1980), and hierarchical clustering (average linkage, percentage difference, dissimilarity) were used for further approximations of plot groupings. All community types were field-validated by ecologists not associated with the study, and proposed community redefinitions were then incorporated into the classification. Community types were named after the dominant species or genera.

Coarse-Scale Landcover Distribution

Coarse-scale gradients of landcover classes were evaluated across each surface age. Landcover classes

were stereoscopically interpreted from 1974 1:15,840 true color aerial photographs on the mature supra-tidal surface and 1986 1:15,840 color infrared air photos on both the young tidal and young supra-tidal surfaces. Ten transacts were extended across each surface perpendicular to the coastline, beginning at randomly selected points on a surface's seaward edge. To differentiate landcover changes moving inland, individual transacts were divided into three equal length segments. Landcover and landform (levee or basin) were then stereoscopically interpreted from 100 evenly spaced points per segment (100 pts./segment × 3 segments = 300 pts./transect). The proportion of each landcover category was determined per segment. The plot data used for describing communities were used to improve the landcover interpretations. Landcover classes that could be consistently interpreted from both the true color and color infrared aerial photos were: *Picea sitchensis* forest; *Salix/Alnus crispa* subsp. *sinuata*; *Myrica gale/Salix*; *Myrica gale* bog; herbaceous; *Carex* (water track); bog (mixture of dwarf shrub and herbaceous); dwarf tree bog; unvegetated mudflat; and pond. Landcover distribution on the mature tidal surface was based on descriptions by Crow (1968) and Trainer (1959).

Channel sinuosity was measured on 10 randomly selected channels from each surface. Each channel was divided into first, second, and third order segments. The standard definition of sinuosity (ratio of channel length to valley length) could not be applied due to the lack of a well-defined valley. Consequently, sinuosity was defined as the ratio of length to the length between the beginning and end of the channel.

RESULTS

Vegetation-Based Community Types

A total of 43 community types were identified on the four surface ages (Table 1). Communities defined by Crow (1968) for the mature tidal surface were rearranged using this study's clustering techniques; as a result, Crow's ten community types were reduced to seven. No cover or constancy values are given because Crow used different sampling methods than used here. Forty community types were identified from this study's plot data, four of which were 'crosswalked' to Crow's (1968) types. Fifteen communities were based on a single plot (Table 1 uncommon communities category), and the remaining 28 communities were defined using a mean of six plots per community.

The dendrogram of hierarchical clustering (Figure 2) provided a summary of the classification's clusters. Shrub-dominated plots were distributed on the left side of the dendrogram, graminoids in the middle, and forbs on the right. Further divisions separated clusters based on species dominance, such as *Alnus crispa* and *Carex lyngbyaei*. Plots dominated by *Alnus crispa* graded into the *Salix* cluster due to codominance between the two groups in 38% of the plots. Clusters that could be clearly separated in the dendrogram generally had plots dominated by a single species, including the *Calamagrostis canadensis, Carex sitchensis, Equisetum fluviatile,* and *Menyanthes trifoliata* clusters. The *Myrica gale* cluster had affinities to the *Carex lyngbyaei* cluster due to *Carex lyngbyaei* dominating the graminoid layer in 47% of the *Myrica gale* plots. Forested plots were distributed in the miscellaneous and herb miscellaneous groupings.

Species clusters within the dendrogram showed a strong fidelity for different surface ages (Figure 2). The *Alnus crispa, Calamagrostis canadensis, Carex lyngbyaei* and herbaceous species, *Equisetum fluviatile* and *Menyanthes trifoliata* clusters all occurred on the young supra-tidal surface. The *Carex lyngbyaei* cluster occurred on the young tidal surface, and the *Carex sitchensis* grouping fell predominantly in the mature supra-tidal surface. The ecological amplitude of *Myrica gale* was wide and, consequently, this grouping showed no strong fidelity to any surface.

Surface Age Descriptions

The following subsections describe biotic and abiotic characteristics for each surface age. These include the coarse-scale distribution of landcover classes (tree, *Salix/Alnus crispa,* pond, etc.) across each surface and fine-scale descriptions of communities, soil characteristics, and landform.

Young Tidal Surface. Coarse-scale landcover classes on the young tidal surface, moving inland, generally changed from a mosaic of the herbaceous and mudflats classes, to herbaceous, then a mixture of shrub (*Salix/Alnus crispa, Myrica gale/Salix*) and herbaceous classes (Table 2, Figure 3). Average total cover of unvegetated mudflat, moving inland, decreased from 65% to 6%; the herbaceous class increased from 35% to 56%; and the total shrub class increased from 0% to 37%. Trees were not encountered on the surface.

At the finer scale, the primarily herbaceous community types on the surface's seaward edge were *Puccinellia nutkaensis* and *Carex lyngbyaei/Potentilla egedii* (Table 1). Further inland, the *Carex lyngbyaei/Potentilla egedii* community dominated, followed by *Myrica gale/Carex lyngbyaei/Equisetum pratense.*

Soil characteristics were relatively consistent between communities. Surface organic matter was typically sparse or absent on most plots (Table 3). Three plots from the *Myrica gale/Carex lyngbyaei/Equisetum*

Table 1. Community type constancy (total plots per community type/total plots per surface) on four surface ages. Community types are ordered on a wet to dry gradient by surface. Crow's (1968) data are representative of the mature tidal surface; only presence (+) absence (. . .) data are presented because different sampling methods were used.

Community Types	Landform	Surface			
		Young Tidal	Mature Tidal	Young Supra-tidal	Mature Supra-tidal
Years since uplift		30	352	30	280
Puccinellia nutkaensis (Presl) Fern. & Weath.	tide flat	10	. . .	. . .	. . .
Potentilla egedii Wormsk./*Deschampsia beringensis* Hult.	tide flat	10	. . .	. . .	. . .
Carex lyngbyaei Hornem./*Potentilla egedii*	tide flat	43	. . .	. . .	. . .
Eleocharis palustris (L.) Roem. & Schult.	tide flat/ basin	3	. . .	6	. . .
Myrica gale L./*Carex lyngbyaei/Equisetum pratense* Ehrh.	upper tide flat/basin	13	. . .	4	. . .
Hippurus tetraphylla L.	tide flat/ basin	3	+	. . .	. . .
Hedysarum alpinum L.-*Deschampsia beringensis*	levee	. . .	+	. . .	. . .
Myrica gale dominated	levee	. . .	+	. . .	. . .
Salix spp.-*Festuca rubra* L.	levee	. . .	+	. . .	. . .
Hippuris vulgaris L.	basin	. . .	+	6	. . .
Carex lyngbyaei	basin	. . .	+	10	. . .
Equisetum fluviatile L. Ampl. Ehrh.	basin	. . .	. . .	10	. . .
Potentilla palustris (L.) Scop./*Equisetum fluviatile*	basin	. . .	. . .	3	. . .
Menyanthes trifoliata L./*Equisetum fluviatile*	basin	. . .	. . .	4	. . .
Carex lyngbyaei/Lathyrus palustris L./*Sphagnum*	basin	. . .	. . .	16	. . .
Calamagrostis canadensis (Michx. Beauv.)/*Lupinus nootkatensis* Donn	levee	. . .	. . .	4	3
Myrica gale/Epilobium angustifolium L.	levee	. . .	. . .	3	. . .
Salix arctica Pall./*Carex lyngbyaei*	levee	. . .	. . .	4	. . .
Salix hookeriana Barratt/*Equisetum arvense* L./*Calamagrostis canadensis*	levee	. . .	. . .	3	3
Alnus crispa (Ait.) Pursh subsp. *Sinuata* (Regel) Hult./*Equisetum arvense*	levee	. . .	. . .	10	. . .
Salix barclayi Anderss./*Equisetum arvense/Calamagrostis canadensis*	levee	. . .	. . .	4	7
Carex pluriflora Hult.-*Carex lyngbyaei/Sphagnum*	basin	. . .	. . .	1	21
Carex sitchensis Prescott/*Eriophorum angustifolium* Honck./*Sphagnum*	basin	. . .	. . .	. . .	21
Oxycoccus micrcarpus Turcz./*Sphagnum*	basin	. . .	. . .	. . .	7
Andromeda polifolia L./*Carex plurifolia/Sphagnum*	basin	. . .	. . .	. . .	7
Myrica gale/Carex pluriflora/Sphagnum	basin	. . .	. . .	. . .	10
Picea sitchensis (Bong.) Carr./*Myrica gale/Carex sitchensis/Sphagnum*	basin	. . .	. . .	. . .	7
Picea sitchensis/Echinopanax horridum (Sm.) Decne. & Planch./*Athyrium filix-femina* (L.) Roth	levee	. . .	+	+	7
Uncommon communities**		17	. . .	11	7

** Communities with only one plot sampled were grouped into the Uncommon communities category, and include: on the young tidal surface *Ranunculus cymbalaria* Pursh, *Carex glareosa* Wahlenb., *Deschampsia beringensis, Myrica gale/Equisetum variegatum* Schleich., and *Salix barclayi/Carex pluriflora*; on the young supra-tidal surface *Carex chordorrhiza* Ehrh., *Carex sitchensis, Eriophorum russeolum* E. Fries, *Calamagrostis canadensis/Potentilla palustris, Carex lyngbyaei*/mixed herb, *Athyrium filix-femina, Myrica gale/Carex sitchensis,* and *Picea sitchensis/Alnus crispa*; on the mature supra-tidal surface *Carex livida* (Wahlenb.) Willd./*Trichophorum caespitosum* (L.) Hartm., and mesic forb.

pratense and *Carex lyngbyaei/Potentilla egedii* communities had a 10-cm-thick organic mat, composed primarily of living roots. No A or B horizons occurred. The C horizon was primarily silt loam; however, sand wedges were present in 14% of the plots. All pH values ranged between 7.2 and 8.0 except for one plot with a pH of 5.5. The soil type was Typic Cryaquent.

Elevation differentiation into levees and basins was not detectable at any of the tidal marsh sample sites. Channel pattern was dendritic with no looping of channels (Figure 4). The range in total channel sinuosity was 1.2 to 2.1.

Mature Tidal Surface. At the coarse-scale, Crow (1968) described landcover on levees, moving inland, as changing from herbaceous to *Myrica gale/Salix* dominated then the *Salix/Alnus crispa* and *Picea sitchensis* landcover classes (Table 2). The inland levees

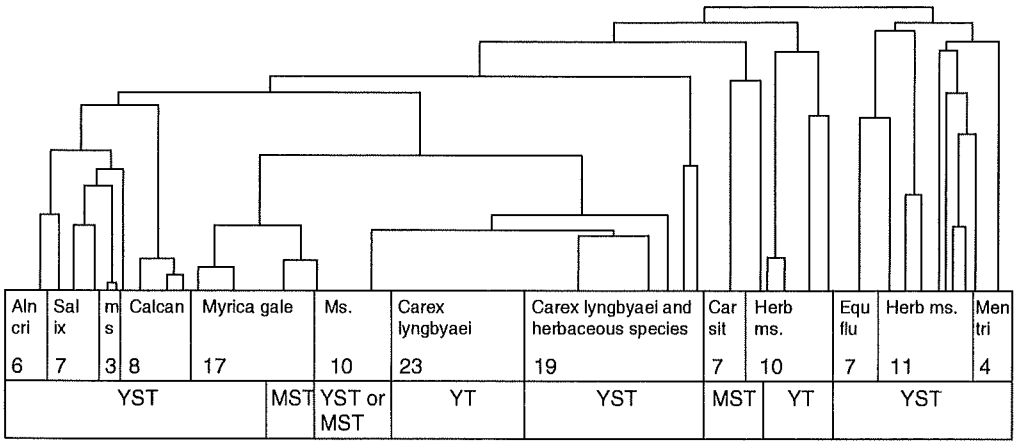

Figure 2. Hierarchical clustering dendrogram for 132 plots sampled on three surface ages. The lower x-axis bar gives the three surface ages (YT = tidal; YST = young supra-tidal; and MST = mature supra-tidal). The upper bar gives general clusterings of vegetation. Species codes are Alncri = *Alnus crispa*; Salix = *Salix* species; Ms = miscellaneous species; Calcan = *Calamagrostis canadensis*; Carsit = *Carex sitchensis*; Equflu = *Equisetum fluviatile*; and Mentri = *Menyanthes trifoliata.*

supporting the *Salix/Alnus crispa* and *Picea sitchensis* classes were rarely (or no longer) tidal and graded into levees of outwash plain landscapes. Basins were dominated by the herbaceous landcover class (Trainer 1959, Crow 1968).

At the finer scale within a levee-basin complex, the seven communities recorded on this surface typically were directly associated with landform (Crow 1968). Levees supported shrub (*Myrica gale* dominated, *Salix* spp.-*Festuca rubra*) or herbaceous (*Hedysarum alpinum-Deschampsia beringensis*) communities, and basins were dominated by the *Carex lyngbyaei* community type (Table 1, Figure 3).

Young Supra-Tidal Surface. Three landcover classes (pond, herbaceous and *Myrica gale/Salix*) dominated basins of the young supra-tidal surface (Table 2). Total cover of only two of these classes changed moving inland—the *Myrica gale/Salix* class (10% to 32%) and the herbaceous class (69% to 43%). Ponds showed no consistent change in cover values moving inland (8% to 13%) and the *Salix/Alnus crispa* class was rare

Table 2. Percent of landcover classes within basins and levees for each surface age. Landcover information for the mature tidal surface is from descriptions by Crow (1968); only presence (+) absence (. . .) data are given. Transect segment codes are Sea = seaward, Mid = mid-surface, and Lan = inland.

	Surface											
	Young Tidal			Mature Tidal			Young Supra-tidal			Mature Supra-tidal		
Landcover	Sea	Mid	Lan	Sea	Mid	Lan	Sea	Mid	Lan	Sea	Mid	Lan
Basins												
mudflat	65	14	6	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
pond	. . .	. . .	. . .	+	+	+	8	13	12	10	8	5
herbaceous	35	63	56	+	+	+	69	56	43	. . .	. . .	. . .
Myrica gale/Salix	0	8	14	. . .	. . .	. . .	10	14	32	. . .	. . .	. . .
Salix/Alnus crispa	0	16	23	. . .	. . .	. . .	<1	<1	<1	. . .	. . .	. . .
Myrica gale bog	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	6	7	12
Carex (water track)	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	5	8	7
bog	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	45	47	46
dwarf tree bog	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	7	8	9
Levees												
herbaceous	. . .	. . .	. . .	+	. . .	. . .	1	2	1	13	5	2
Myrica gale/Salix	. . .	. . .	. . .	. . .	+	. . .	3	5	8	2	3	6
Salix/Alnus crispa	. . .	. . .	. . .	. . .	. . .	+	8	9	4	14	7	4
Picea sitchensis	. . .	. . .	. . .	. . .	. . .	+	. . .	. . .	<1	<1	7	10

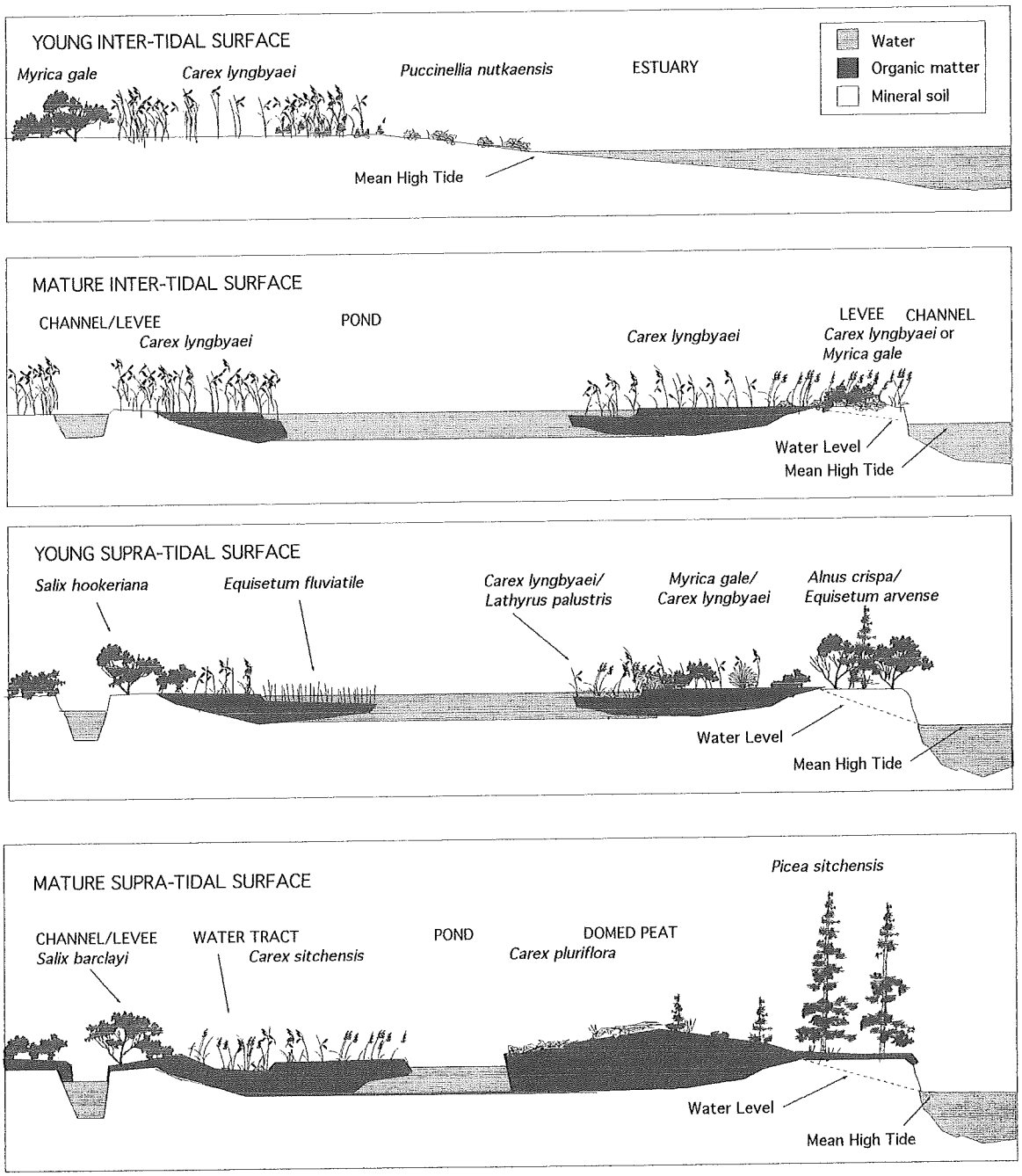

Figure 3. Changes in landform and vegetation on marine deltaic surfaces of increasing age. Mean high tide is given for each surface.

(<1%) within all basins. These changes in landcover classes were not always consistent between transacts.

On levees, moving inland, no consistent pattern of landcover change was observed (Table 2). The dominant classes were *Salix/Alnus crispa* (range of cover values 4–9%), *Myrica gale/Salix* (3–8%), and herbaceous (1–2%).

Channels showed extensive looping, with sinuosity values ranging from 1.5 to 16.4 (Figure 4). The majority of looping occurred in the first order channels and often began where they merged with other streams.

At a finer scale, the 24 communities recorded on this surface showed a consistent zonation within levee-basin complexes moving from levee to basin center (Figure 3). The zonation was directly associated with basin depth and changed from shrub (*Alnus crispa/Equisetum arvense*) or forb (*Calamagrostis canadensis/Lupinus nootkatensis*) on levees to shrub/herbaceous (*Myrica gale/Carex lyngbyaei/Equisetum pra-*

Table 3. Physical site variables on three marine deltaic surface ages. Site information for the mature tidal surface was not available.

	Surface				
	Young Tidal	Young Supra-tidal		Mature Supra-tidal	
Site Variable	Tide Flat	Levee	Basin	Levee	Basin
Organic matter horizon					
Mean depth ± SD (cm)	1.6 ± 3.3	6.2 ± 4.9	18.9 ± 15.2	4.0 ± 3.4	59.2 ± 33.3
Range in depth (cm)	0 to 10	0 to 16	0 to 55	0 to 10	12 to 140
A horizon					
Mean depth ± SD (cm)	NP	1.8 ± 5.5	NP	7.3 ± 3.1	NP
Range in depth (cm)		0 to 23		3 to 12	
Depth to water*					
Mean depth ± SD (cm)	tidal	>−100	+17 ± 23	>−100	−17 ± 22
Range in depth (cm)	tidal	−5 to >−160	+60 to −20	−5 to >−160	+10 to −80
pH of OM horizon					
Mean pH ± SD	7.0**	5.2 ± 0.7	5.8 ± 1.1	4.4 ± 0.3***	
Range in pH		3.8 to 5.9	2.8 to 7.0	4.0 to 5.3	
pH of C horizon					
Mean pH ± SD	7.6 ± 0.7	6.0 ± 1.0	6.3 ± 1.1	5.6 ± 1.1	
Range in pH	5.5 to 8.0	5.3 to 7.2	3.7 to 8.0	5.1 to 6.0	
Mineral soil texture****					
Silty clay loam (<0.05 mm)	0	5	3	0	0
Silt loam (0.002–0.05 mm)	86	67	84	83	79
Loam (0.002–2 mm)	11	5	3	17	0
Sandy loam (0.05–2 mm)	3	23	10	0	21
Number of plots	28	31	18	8	22

NP = Not present.
* Positive values equal water above the ground surface.
** pH was recorded on only one plot with an organic horizon.
*** pH was not recorded on the 30 study plots; the pH values are from 34 plots on similar habitats near the study plots.
**** The percentage of plots dominated by the different soil textures (# plots dominated by soil texture/total plots).

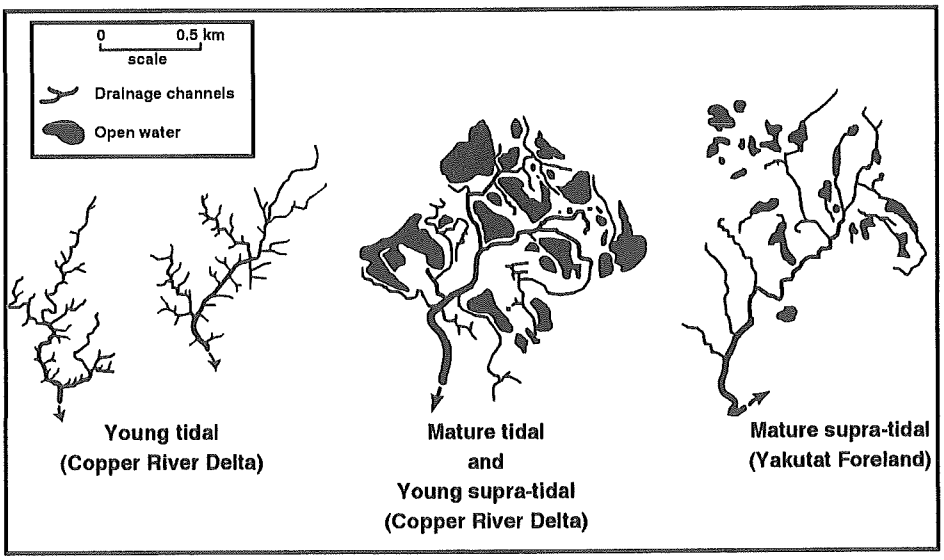

Figure 4. Examples of channel patterns on three marine deltaic surfaces of increasing age. Note that only one pattern is representative of the mature tidal and young supra-tidal surfaces because only minor changes have occurred since the 1964 uplift.

tense) communities on shallow peat deposits bordering the levees to sedge (*Carex lyngbyaei/Lathyrus palustris/Sphagnum* and *Carex lyngbyaei*) and emergent forb communities (*Equisetum fluviatile,* and *Hippuris vulgaris*) on thicker peat to open water in the center of the basin (Table 1). Herbaceous communities occurred on banks of both tidal and non-tidal channels. Not all the vegetation zones were always expressed.

Two trees species, *Populus trichocarpa* Torr. & Gray and *Picea sitchensis,* occurred on levees across the surface. All tree core ages were <28 yrs, excluding cores from the *Picea sitchensis/Echinopanax horridum/Athyrium filix-femina* community, which only occurred on the most inland levees. The age of these young trees showed that they germinated after the 1964 uplift.

Soil profiles and schematic cross sections of physical site characteristics showed a consistent pattern within levees and basins (Table 3; Figure 3). Mineral soils underlaid the general pattern of channels, levees, and basins. The difference in mineral soil elevation between levee top and the basin bottom ranged from 72 to 108 cm (Thilenius 1990, Boggs 1998). Anchored root-mats bordered the mineral soil levees, increased in depth to a maximum of 55 cm moving towards basin center, and formed floating or rooted root-mats on pond edges, with a maximum surface water depth of 60 cm. Within basins, root-mat height did not exceed the maximum water-surface level except for raised root wads (i.e. no domed peat). Water levels in ponds throughout the uplifted marsh were often filled to the surface of their levees except during extended periods of low precipitation. The water table on levees was typically not reached in a standard 100 cm soil pit due to a lowering of the water level as it drained from the basins, through the levees, and into the adjacent, and lower, channels.

Silt loam dominated soils were more common within basins (87% constancy) than on levees (72% constancy; Table 3). Within basins, the pH of the organic and underlying C horizon averaged 5.8 ± 1.1 and 6.3 ± 1.1, respectively. On levees, A horizons occurred in 17% of the plots, and B horizons were not present. Basin soil types were predominantly Typic Hydraquents, Hydric Borofibrists, Terric Borohemists, Typic Borofibrists, and Histic Cryaquepts. Levee soil types included Typic Cryaquepts, Hydric Borohemists, Humic Typic Cryofluvents, and Typic Cryofluvents.

Mature Supra-Tidal Surface. Coarse-scale landcover changes were evident, moving inland, on both basins and levees of the mature supra-tidal surface (Table 2). Within basins, cover of the pond class decreased from 10% to 5%, the *Myrica gale* bog class increased from 6% to 12%, and the remaining landcover classes remained relatively constant. On levees, moving inland, total cover of both the herbaceous and *Salix/Alnus crispa* classes decreased 13% to 2% and 14% to 4%, respectively. Conversely, landcover of both the *Picea sitchensis* and *Myrica gale/Salix* classes increased <1% to 10% and 2% to 6%, respectively.

Tidal and freshwater channels showed extensive looping, with sinuosity values ranging from 1.5 to 10.4 (Figure 4). The majority of looping occurred in the first order channels. However, this channel pattern was more muted than on the young supra-tidal surface due to paludification covering and hiding many of the first order channels.

Several factors indicated that the current channels occupy the pre-uplift tidal channels. Channel bottoms were still mineral soil, and levee peat depth was shallow, suggesting drier conditions than in the adjacent thicker basin deposits (Table 3). The looped channels also indicated that they were formed during tidal marsh development.

At the finer scale, the spatial pattern of the twelve communities identified on this surface corresponded to landform position (Table 1). Levees supported mature tree (*Picea sitchensis/Echinopanax horridum/Athyrium filix-femina*), shrub (*Salix barclayi*), and herbaceous (*Calamagrostis canadensis*) dominated communities. Domed bogs were primarily dominated by the dwarf tree community *Picea sitchensis/Myrica gale/Carex sitchensis/Sphagnum,* and water tracks were dominated by sedge communities (*Carex pluriflora-Carex lyngbyaei/Sphagnum* or *Carex sitchensis/Eriophorum angustifolium/Sphagnum*). This zonation was not expressed in all levee-basins.

Within basins, peat accumulation has led to domed bogs, water tracks, and peat-bordered ponds. Ponds ranged in depth to > 140 cm, and basin peat averaged 59.2 ± 33.3 cm, ranging up to 140+ cm thick (Figure 3, Table 3). Water tracks occupied lower positions within the basins, and domed peat height often exceeded that of levees. Depth to water table ranged from 10 cm above the surface to 80 cm below. The pH of the organic layer averaged 4.4 ± 0.3. The underlying mineral soils within basins were silt loam (79% of pedons), with the remainder loam or sandy loam. Soil types were Terric Cryohemists, Typic Cryohemists, Fluvaquent Cryohemists, Terric Cryofibrists, Typic Cryaquents, and Histic Cryaquepts.

Levee soils were characterized by an organic layer ranging from 0 to 10 cm thick over silt loam or sandy loam (Table 3). The water table was not reached in 75% of the soil pits. As on levees of the young supratidal marsh, depth to water table was lower due to a lowering of the water level as it drained through the levees into the adjacent, lower channels. Silt loam soils dominated 83% of the levee pedons, with the remain-

der loam or sandy loam. Soil types included Typic Cryaquepts, Oxyaquic Cryorthents, and Typic Cryaquents.

DISCUSSION

O'Neill et al. (1986) stress the importance of viewing the world in the spatial and temporal scale at which it responds rather than the spatial and temporal scale relevant to land managers (<100 yrs). This approach is critical for understanding the origins and successional trajectory of marine deltaic landscapes in Alaska. The primary disturbance dynamics that form a marine deltaic landscape often no longer exist within the spatial boundaries of a single deltaic surface. Consequently, the successional trajectory of an uplifted marsh cannot be determined from observations within its boundaries because all of the seral stages and processes are not present.

Landscape Evolution

Our results present a sequence of vegetation and landform evolution on marine deltaic deposits of increasing age (Figure 3). Prior to our study, Crow (1971), Morrison (1984), and Thilenius (1990, 1995) presented hypotheses on vegetation succession on this landscape without the benefit of studying separate surface ages. They suggested that after a tidal marsh matures and is uplifted, the herbaceous and shrub vegetation of levees will be displaced by trees or shrubs and that poorly drained inter-levee basins will develop into peatlands.

Our empirical results support their hypotheses. Within three years after the 1964 uplift of mudflats, tide-tolerant species (*Puccinellia nutkaensis, Carex lyngbyaei*) established on new inland locations (Figure 3; Crow 1968). Pioneer swards of *Carex lyngbyaei* were oval in outline and expanded annually until the individual swards coalesced into larger units (Thilenius 1990), eventually dominating the marsh. In the western portion of the marsh after 15 yrs and 30 yrs, the sedge marsh extended over 1 km and 2 km seaward, respectively. Fifteen yrs post-uplift, the inland *Carex lyngbyaei* sites were in turn beginning to be invaded by shrubs such as *Salix* spp. and *Myrica gale* (Thilenius 1990). Thilenius (1990), Batten et al. (1978), Morrison (1984), Vince and Snow (1984), Rosenberg (1986), and del Moral and Watson (1978) all described tidal communities within south-central Alaska that were similar to communities described here.

Levees, basins, and channels develop as the tidal marsh ages. Water slowed at the sward edges causes high rates of deposition, typically of the coarser sediments. Less sediment is available for deposition in the middle of the sward further removed from the channel. These differential accretion rates, and stabilization by the vegetation, lead to the formation of levees (on the edge of the swards and channels) and basins. Benda et al. (1991) estimated that differential accretion leading to the formation of levees and basins was occurring on the young tidal surface at the rate of 0.06 cm/yr, but noted that levees and basins were, as of yet, not detectable.

Tidal channels on the young tidal surface are formed through a combination of previously established drainage patterns and the coalescing of adjacent swards of *Carex lyngbyaei* (Steers 1977). The channels become more entrenched as the surface height of levees increases (Figure 4). The average accretion rate on the Copper River Delta tidal marsh is estimated at 4 mm/yr (Benda et al. 1991), and the surface is submerging at 4.5–6.5 mm/yr (Plafker et al. 1990). In time, accretion may match the submergence rate, and because soil-surface height is a function of water height, it may eventually equilibrate at high tide level.

As the tidal surface matures, *Carex lyngbyaei* continues to dominate the basins, forming a thick rootmat, the surface of which is often level with the levees (Figure 3). These observations are supported by Trainer (1959), Crow (1968), and aerial photo (1959 1:15,840 black and white) interpretations of vegetation in the middle segment of the surface by Stephenson (1995). On levees, *Carex lyngbyaei* is replaced by herbaceous and shrub species (*Hedysarum alpinum, Deschampsia beringensis, Myrica gale, Salix* spp., and *Festuca rubra*). Species better adapted to colonizing mudflats (*Puccinellia nutkaensis* and *Ranunculus cymbalaria*) decrease as the marsh ages.

After the 1964 tectonic uplift of the mature tidal surface, loss of the tidal influence initiated abrupt changes in vegetation composition and structure (Crow 1968, Batten et al. 1978, Thilenius 1990, 1995, Davidson and Klinge 1992, Stephenson 1995, Boggs 1998). Saltwater-intolerant species (such as *Lathyrus palustris* and *Equisetum fluviatile*) invaded the basins. Some tidal marsh species (*Triglochin maritimum* L. and *Hedysarum alpinum*) described as common in previous studies (Trainer 1959, Crow 1968) are now rare. However, *Carex lyngbyaei* remains a dominant species within the basins. Development of ombrotrophic peat conditions is suggested by the invasion of species (*Andromeda polifolia, Sphagnum* spp.) characteristic of nutrient-poor peatlands.

On levees of the young supra-tidal surface, shrub (and some herbaceous) dominated communities displace all the previously described communities (Table 1; Crow 1968). *Alnus crispa* is the dominant early seral species just as it is on disturbed surfaces of the region, such as avalanche paths and new alluvial de-

posits (DeVelice et al. 1998). Saplings and seedlings of two tree species (*Populus trichocarpa* and *Picea sitchensis*) are also found on levees and are common disturbance-induced species found on other landscapes of the region. We attribute this abrupt change in community composition to the loss of periodic tidal inundation and the probable lowering of the water table on levees.

On the mature supra-tidal surface, species typical of peatlands for the region increase in dominance, including *Empetrum nigrum* L., *Vaccinium uliginosum* L., *Carex pluriflora,* and *Sphagnum* spp. Species that initially invade the young supra-tidal surface (*Populus trichocarpa, Alnus crispa, Calamagrostis canadensis, Equisetum arvense, Equisetum fluviatile,* and *Lathyrus palustris*) decrease in cover as the surface ages. Their limited occurrence on the mature supra-tidal surface is likely a function of available disturbance patches.

Pedogenic diversity increases as the landscape ages, from one soil subgroup on the young tidal surface to nine subgroups on the oldest two surfaces (Table 3). This is due to profile development on peat and mineral soils, such as the development of B horizons and the development of ombrotrophic, in addition to minerotrophic, peatlands. Peat thickness in basins tripled between the young and mature supra-tidal surfaces. As expected with increased age, decompositional attributes of peat changed from root-dominated to histic or sapric *Sphagnum* spp. dominated. However, root-mats persisted within fens on the mature supra-tidal surface.

Nearly all basins on the young supra-tidal surface seemed to be minerotrophic, with slightly acidic organic soils (pH 5.8 $\pm$ 1.1), but average pH decreased to 4.4 $\pm$ 0.3 on the mature supra-tidal surface. On the mature supra-tidal surface, the increase in peat depth and decrease in pH indicates an ombrotrophic environment. However, most basins support some sites with minerotrophic characteristics, such as elevated pH, species typical of fens (*Menyanthes trifoliata, Equisetum fluviatile*), and ponded stringers due to partial damming of drainage ways. Ponds persist on the mature supra-tidal surface, although encroachment by peat reduces their size.

Our observations suggest that filling of the basins through time is a result of sedimentation in addition to peat buildup. The dominant sediment inputs are from loess blown in from unvegetated glacial outwash deposits and flooding from glacial outwash distributory channels. Field observations and aerial photo interpretation show that the sediment-rich glacial rivers flood ponds adjacent to channels on the inland supra-tidal surface during high flows. Water in ponds and first order streams further removed from outwash channels and more seaward were always clear, indicating low sediment loads. Consequently, we suggest that only those ponds adjacent to distributory channels on the inland supra-tidal surface have significant sediment inputs from glacial streams. Erosion along channel levees was also observed as a result of direct bank erosion from tidal flow and undercutting and failure of large blocks (Stanley et al. 1966). However, rates of erosion on the surface are unknown.

Our understanding of landscape evolution improved when the spatial distribution of vegetation and physical site variables were incorporated. For example, within basin-levee complexes, we were able to follow the development of communities because they were strongly linked to landform position (levee top, levee-basin edge, shallow basin, etc.). At the landscape scale, vegetation gradients across a surface enabled us to track differential development of communities on inland versus seaward levees. This differential succession suggests that many pathways of community succession could be represented along the chronosequence (Mann et al. 1995). The particular sequence followed at any place on a surface would depend heavily on the interaction of physical variables (slope, hydrology) and the unique history of vegetation for the site.

A limitation of our study was that inadequate information was available to explain certain observations. For example, we have no intermediate stages (i.e., surfaces) that show the formation of water tracks and domed bogs on the mature supra-tidal surface. In the absence of observed data, we can only hypothesize how these significant features formed. Also, our study did not address other successional sequences as a result of perturbation factors (blowdown, disease, herbivory) other than tectonic uplift. For example, beaver (*Castor canadensis* Kuhl) and moose populations have increased on the young supra-tidal surface as a result of the invasion of woody vegetation (MacCracken 1992, Stephenson 1995). These herbivores can severely affect vegetation composition by high-grading certain species. Although beaver and moose may be only a short-lived phenomenon in the overall time scale of the chronosequence–both are rare in tidal systems, common in minerotrophic peatlands, and rare in ombrotrophic peatlands–their current impact may have long-lasting consequences on site composition and peat accumulation. However, successional stages influenced by beaver and moose were considered secondary to the overwhelming influence of peat accumulation in basins and to forest and shrub development on levees.

Relict Species and Communities

Some species persist on older surfaces as relicts from previous tidal communities, showing the importance of history in the occurrence of communities.

Carex lyngbyaei dominates tidal marshes of south-central and southeast Alaska but rarely occurs on non-deltaic surfaces and only as sporadic small clones. However, on our study surfaces, it persisted 280+ yrs after tidal conditions no longer occurred (Table 1). *Carex lyngbyaei* canopy cover decreases six fold (37% to 6%) from the young tidal to the mature supra-tidal surface. However, *Carex lyngbyaei* is still dominant (18% cover) in the *Carex pluriflora-Carex lyngbyaei/ Sphagnum* community on the mature supra-tidal surface (Table 1).

Salix hookeriana is another tidal species that persists on supra-tidal surfaces. It is found only on coastal landscapes, typically on the extreme high tide zone of levees (Viereck and Little 1972). Several tidal species, such as *Puccinellia nutkaensis* and *Triglochin maritima,* show poor persistence and could no longer be found on even the youngest supra-tidal surface (30 yrs old). Other species, such as *Myrica gale* and *Salix barclayi*, occur on both tidal (extreme high tide zone) and supra-tidal surfaces, but their persistence cannot be evaluated from this study because they regenerate in non-tidal environments.

Viewing a Surface Age as a Successional Stage

In this study, tectonic uplifts led to perturbation of entire marine-deltaic surfaces at specific points in time. This is an unusual situation, where an entire surface responds vegetatively and geomorphically as a single disturbance patch (Turner et al. 1994). These landscape-scale disturbance patches can be interpreted as seral stages within a landscape successional sequence, moving from young tidal surface through mature supra-tidal surface. Of interest would be an estimation of the seral balance of this landscape across coastal Alaska (Watt 1947, Bormann and Likens 1979). Intertidal surfaces are rare along the Gulf of Alaska, yet they are critical for the maintenance of tidal species of the region (Crow 1971, Campbell 1990). However, this seral equilibrium cannot be estimated until the frequency and spatial distribution of the region's tectonically uplifted marine deltaic landscapes are further evaluated.

Linking the concept of seral equilibrium at a landscape scale to a finer spatial scale of community type and species is important for conservation purposes (Bougeron 1988). Many plant communities occur in only one of the four chronosequence stages, making the tectonic creation of new young surfaces a possible prerequisite for the long-term survival of these communities (Table 1). In all, communities defined in this study have a high fidelity for specific surface ages, with 74% of the major communities occurring in only one surface Age. Many of these communities occur on other landscapes of the region, such as dunes and outwash plains. However, some communities exist only on the marine deltaic landscape, such as the six communities with *Carex lyngbyaei* as a dominant or co-dominant species (Shephard 1995, Boggs 1998). Specific fauna and flora are often dependent on these communities, and predictions of their distribution and stability are linked to that of the community and landscape.

The results show that each marine deltaic surface age has consistent patterns in vegetation, landform, and soils at both the basin-levee and landscape scales. To a large degree, this consistency in pattern enables us to view each surface age as a unit for management and research purposes when evaluating specific environmental factors, such as vegetation succession and landform and soil development. These findings help us link into the development of hierarchical landscape units that are being described and delineated for management and research purposes within Alaska (Omernik 1987, Ecomap 1994). Yet, for these units to be useful, we must understand at what scale we can expect generality and predictability in pattern as well as the processes controlling these patterns (Odum 1969, Swanson et al. 1988, Walker and Walker 1990, McAuliffe 1994, Weiner 1995). Our study addresses this issue by linking fine-scale successional sequences and landform development to the vegetation and landform patterns found on entire marine deltaic surfaces.

Our study represents one general successional pathway for these surfaces. As the Copper River Delta's supra-tidal marsh matures it may well support vegetation somewhat compositionally different than that found on the mature landscapes of the Yakutat Foreland. This is partially due to past and present climate fluctuations (Little Ice-Age, global warming) affecting species that will continue to migrate or die out of the region whether the climate of coastal Alaska warms or continues its post-hypsithermal cooling trend (Pielou 1991). Furthermore, inter-surface differences in environmental variables (nutrients, hydrology, acidity) may affect rates of peat development and species composition. However, even with these potential fluctuations in climate, species, and site variables, we expect the general pattern of landscape evolution given in this paper to persist.

ACKNOWLEDGMENTS

Financial support was provided by the United States Department of Agriculture Chugach National Forest, Chatham Area of the Tongass National Forest, Alaska Natural Heritage Program (University of Alaska Anchorage), and The Nature Conservancy. We thank Robert DeVelice, Jon Martin, Dan Logan, Mike Novy,

and Gerald Tande for supporting the project. We are grateful to Dennis Fuster, Brent Fagan, Einav Shochat, Bill Queitzsch, Fransisco Escobedo, Mike Baxter, Brent Davis, Don Youkey, and John Crouse for field assistance, and Kitty LaBounty for identification of bryophytes. Robert DeVelice, David Duffy, and L. R. Walker provided valuable review comments.

LITERATURE CITED

Batten, A. R., S. Murphy, and D. F. Murray. 1978. Definition of Alaskan coastal wetlands by floristic criteria. Corvallis Environmental Research Lab, Corvallis, OR, USA. EPA804965–01.

Benda, L., T. Lisle, and K. Sullivan. 1991. A reconnaissance of the fluvial geomorphology of the Copper River Delta. p. 18–23. *In* M.D. Bryant (ed.) The Copper River Delta Pulse study: An interdisciplinary survey of the aquatic habitats. United States Department of Agriculture, Corvallis, OR, USA. Forest Service General Technical Report PNW-GTR-282.

Boggs, K. 1998. Classification of community types, successional sequences and landscapes of the Copper River Delta, Alaska. United States Department of Agriculture, Corvallis, OR, USA. Forest Service General Technical Report. (In press).

Bormann, F. H. and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, NY, USA.

Bougeron, P.S. 1988. Advantages and limitations of ecological classification for the protection of ecosystems. Conservation Biology 2:218–220.

Brown, D. 1954. Methods of surveying and measuring vegetation. Commonwealth Agricultural Bureau, Bucks, England. Bulletin 42.

Campbell, B.H. 1990. Factors affecting the nesting success of dusky Canada geese, *Branta canadensis occidentalis,* on the Copper River Delta, Alaska. The Canadian Field-Naturalist 104:567–574.

Crow, J. H. 1968. Plant ecology of the Copper River Delta, Alaska. Ph.D. Thesis. Washington State University, Pullman, WA, USA.

Crow, J. H. 1971. Earthquake-initiated changes in the nesting habitat of the dusky Canada goose. p. 130–136. *In* The great Alaska earthquake of 1964: Biology. National Academy of Sciences, Washington, DC, USA.

Daubenmire, R. D. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–66.

Daubenmire, R. D. 1968. Plant Communities. Harper and Row, Publishers, New York, NY, USA.

Davidson, D. and K. Klinge. 1992. Copper River Delta integrated inventory. United States Department of Agriculture Chugach National Forest, Anchorage, AK, USA.

del Moral, R. and A. F. Watson. 1978. Vegetation of the Stikine flats, southeast Alaska. Northwest Science 52:137–150.

DeVelice, R., C. Hubbard, K. Boggs, S. Boudreau, M. Potkin, and T. Boucher. 1998. Plant community types of the Chugach National Forest: South-central Alaska. Review Draft. United States Department of Agriculture, Chugach National Forest, Anchorage, AK, USA.

Ecomap. 1994. Ecological subregions of the United States: section descriptions. United States Department of Agriculture, Washington, DC, USA.

Hampton, M. A., P. R. Carlson, H. J. Lee, and R. A. Feely. 1987. Geomorphology, sediment, and sedimentary processes. p. 93–114. *In* D.W. Hood and S. T. Zimmerman (eds.) The Gulf of Alaska. Physical environment and biological resources. United States Department of Commerce and United States Department of the Interior, Washington, DC, USA.

Hill, M. D. 1979. TWINSPAN: a Fortran program for arranging multivariant data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics Department, Cornell University, Ithaca, NY, USA.

Hill, M. D. and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

Holloway, R. G. 1990. Pollen and plant macrofossil analyses of 49YAK19 (D'yaguna'et) and 49YAK20 (Shallow Water Town) Yakutat, Alaska. Castetter laboratory for ethnobotanical studies technical series. United States Department of Agriculture, Juneau, AK, USA. Tongass National Forest Report 283.

Hulten, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, CA, USA.

Mann, D., C. L. Fastie, E. L. Rowland, and N. H. Bigelow. 1995. Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. Ecoscience 2:184–199.

MacCracken, J. G. 1992. Ecology of moose on the Copper River Delta, Alaska. Ph.D. Dissertation. University of Idaho, Moscow, ID, USA.

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. Ecological Monographs 64:11–148.

Molnia, B. F. 1986. Glacial history of the northeastern Gulf of Alaska—a synthesis. p. 219–236. *In* T.D. Hamilton, K.M. Reed, and R.M. Thorson (eds.) Glaciation in Alaska, the Geologic Record. Alaska Geological Society, Anchorage, AK, USA.

Morrison, J. 1984. Evaluation of the vegetative composition of the tidal marsh at Neka Bay and its related use by wildlife. United States Department Agriculture Tongass National Forest, Sitka, AK, USA.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York, NY, USA.

National Climatic Data Center. 1993. Local climatological data for Yakutat, Alaska. Environmental Data Service, National Oceanic and Atmospheric Administration, Ashville, NC, USA.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Omernik, J.M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118–125.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, NJ, USA.

Pfister, R. D. and S. F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science 26:52–70.

Pielou, E. C. 1991. After the Ice Age: The Return of Life to Glaciated North America. The University of Chicago Press, Chicago, IL, USA.

Plafker, G., K. R. Lajoie, and M. Rubin. 1990. Determining the recurrence intervals of great subduction zone earthquakes in southern Alaska by radiocarbon dating. p. 1–14. *In* R. E. Taylor, A. Long, and R. Kra (eds.) Radiocarbon after Four Decades. University of Arizona Press, Tucson, AZ, USA.

Potyondy, J., J. Meyer, and A. Mace, Jr. 1975. An analysis of 1964 earthquake effects upon the vegetation and hydrology of the Copper River Delta, Alaska. Institute of Agriculture, University of Minnesota, Minneapolis, MN, USA. Report 75–6.

Reimnitz, E. 1966. Late Quaternary history and sedimentation of the Copper River Delta and vicinity. Ph.D. Dissertation. California University, San Diego, CA, USA.

Rosenberg, D. H. 1986. Wetland types and bird use of Kenai lowlands. Special Studies, United States Fish and Wildlife Service, Region 7, Anchorage, AK, USA.

Searby, H.W. 1969. Coastal weather and marine data summary for Gulf of Alaska, Cape Spencer westward to Kodiak Island. United States Department of Commerce, Silver Spring, MD, USA. ESSA Technical Memorandum EDSTM 8.

Shephard, M. E. 1995. Plant community ecology and classification of the Yakutat foreland, Alaska. United States Department of Agriculture, Sitka, AK, USA. Tongass National Forest Technical Report R10-TP-56.

Stanley, D. J., E. L. Krinitzsky, and J. R. Compton. 1966. Mississippi River bank failure, Fort Jackson, Louisiana. Geological Society America Bulletin 77:850–866.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Company, Inc., New York, NY, USA.

Steers, J. A. 1977. Physiography. p. 31–60. *In* V.J. Chapman (ed.) Wet Coastal Ecosystems. Elsevier, Amsterdam, the Netherlands.

Stephens, F. R. and R. F. Billings. 1967. Plant communities of a tide-

influenced meadow on Chichigof Island, Alaska. Northwest Science 41:178–183.
Stephenson, T. R. 1995. Nutritional ecology of moose and vegetation succession on the Copper River Delta, Alaska, Ph.D. Dissertation. University of Idaho, Moscow, ID, USA.
Stevens, P. R. and T. W. Walker. 1970. The chronosequence concept and soil formation. The Quarterly Review of Biology 45:333–350.
Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38:92–98.
Thilenius, J. F. 1990. Woody plant succession on earthquake-uplifted coastal wetlands of the Copper River Delta, Alaska. Forest Ecology and Management 33/34:439–462.
Thilenius, J. F. 1995. Phytosociology and succession on earthquake-uplifted coastal wetlands, Copper River Delta, Alaska. United States Department of Agriculture, Portland, OR, USA. Pacific Northwest Research Station General Technical Report PNW-GTR-346.
Trainer, C. E. 1959. The 1959 western Canada goose (*Branta canadensis occidentalis*) study on the Copper River Delta, Alaska. p. 1–9. *In* United States Bureau of Sport Fish, Wildlife, Mines. Annual Waterfowl Report: Alaska, USA.
Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171–197.
Turner, M. G., W. H. Romme, and R. H. Gardner. 1994. Landscape disturbance models and the long-term dynamics of natural areas. Natural Areas Journal 14:3–11.
USDA Soil Survey Staff. 1975. Soil taxonomy—a basic system of soil classification for making and interpreting soil surveys. United States Government Printing Office, Washington, DC, USA. United States Department of Agriculture Handbook 436.
Viereck, L. A. and E. L. Little. 1972. Alaska Trees and Shrubs. United States Department of Agriculture, Washington, DC, USA. Agriculture Handbook No. 410.
Vince, S. W. and A. A. Snow. 1984. Plant zonation in an Alaskan salt marsh: I. distribution, abundance, and environmental factors. Journal of Ecology 72:65–667.
Vitt, D. H., J. E. Marsh, and R. B. Bovey. 1988. Mosses, Lichens and Ferns of Northwest North America. Lone Pine Publishing, Edmonton, Alberta, Canada.
Walker, D.A. and M. D. Walker. 1990. History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: a hierarchical approach to analyzing landscape change. Journal of Applied Ecology 28:244–276.
Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1–22.
Weiner, J. 1995. On the practice of ecology. Journal of Ecology 83: 153–158.
Witten, E. 1996. The role of a Sitka spruce (*Picea sitchensis*) population in plant community succession following tectonic uplift of the Copper River Delta, Alaska. M.S. Thesis. Yale School of Forestry and Environmental Studies, New Haven, CT, USA.
Yehle, L. A. 1975. Preliminary report on the reconnaissance engineering geology of the Yakutat area, Alaska, with emphasis on evaluation of earthquake and other geologic hazards. United States Geological Survey Open-File Report 75–529.

Manuscript received 12 June 1997; revision received 20 April 1998; accepted 19 June 1998.