



PLANT SUCCESSION ON DISTURBED SITES, NORTH SLOPE, ALASKA, U.S.A.*

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ABSTRACT

Early plant succession was examined on a crude-oil damaged wet-sedge meadow, abandoned silt loam roads, and on drilling pads at exploratory wellsites on Alaska's North Slope. Phosphorus fertilization encouraged *Carex aquatilis* and *Dupontia fisheri* recolonizing and replacing of seeded *Puccinellia borealis* where crude-oil damage had occurred 14 yr earlier. After 10 yr, plant cover of graminoids and moss was sufficient to reduce active layer depth about 3.0 cm. On barren, reworked silt loam, phosphorus fertilization promoted natural recolonization. Without fertilization, canopy cover averaged about 65%; with phosphorus fertilization canopy cover averaged over 100%. Bare ground (absence of litter basal and/or plant cover) averaged about 40% without phosphorus fertilization, and with phosphorus, bare ground averaged 12%.

Twelve drilling pads constructed 5 to 8 yr earlier were examined for colonizing species. Various combinations of *Arctagrostis latifolia*, *Poa glauca*, *Poa pratensis*, and *Festuca rubra* had been seeded. *Poa pratensis* consistently failed. The other three species usually became established. Species diversity of natural pioneering plants was largest on pads in the foothills. Colonization was poorest on unstable sands, saline substrates, and at locations intensely grazed by geese and caribou on the coastal plain. Thirty-six forb, 30 graminoid, and 7 shrub species were colonizing one or more of the drilling pads. Frequent colonizers were (forbs) *Senecio congestus*, *Artemisia tilesii*, *Cochlearia officinalis*, *A. alaskana*, *A. borealis*, and *Descurainia sophioides*. Frequent pioneering grasses, in addition to the three seeded species, were *Arctophila fulva*, *Alopecurus alpinus*, and *Phippsia algida*. *Salix planifolia* ssp. *pulchra* was the only shrub colonizing on two or more pads.

INTRODUCTION

Plant succession on man-caused disturbed areas on Alaska's North Slope is a topic of relatively recent significance, essentially beginning with the discoveries of major hydrocarbon resources at Prudhoe Bay. With the

hydrocarbon developments came terrain perturbations that were of scales and types previously absent from the natural environment. These included construction of thick gravel pads, airstrips and roadbeds, physical damage to soils and plant cover, and the impact of oil spills. Such sites offered an array of substrate conditions for

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plant colonization that varied from gravel lacking fine components to physically mixed silt alluvium and intact soils which had been chemically altered by crude oil and refined petroleum products. If and how plants colonize those sites became a concern for land managers and operators of the oil fields and related facilities.

Potter (1972) reported that *Poa arctica* was a major colonizer on coastal sites which had been disturbed by aboriginal culture. Most of the information available on plant succession in the region is from the tussock tundra, which is located inland and beyond major oil field construction sites. Some of the earliest observations of plant succession (1946–1951) were documented by Spetzman (1959). He noted a possible hydrarch succession for arctic ponds that predominate on the coastal plain, and he described a tussock tundra successional sequence for the inland and foothills vegetation.

Bliss and Cantlon (1957) observed tussock tundra succession on river alluvium along the Colville River in 1953. Other information on tundra succession could be extrapolated from studies conducted elsewhere in Alaska or Canada such as work by L. A. Palmer near Unalakleet, Alaska (Pegau, 1970). Pegau (1970) reexamined Palmer's 1929 spaded plot in 1965. After 36 yr, the plot was only 40% covered with *Dryas* and moss. Those plants seemed to have invaded from the margin of the disturbance rather than by establishing new plants from seed and spores. In contrast, a rapid recolonization by seedlings was observed more recently in overgrazed muskox pastures and a trampled corral near Unalakleet (McKendrick, 1981).

Everett et al. (1985) studied recolonization of 20-yr-old, man-caused disturbances in the Cape Thompson area and noted several prominent invaders: *Deschampsia caespitosa*, *Sagina nivalis*, *Oxytropis nigrescens*, *Silene acaulis*, *Carex bigelowii*, *Arctagrostis latifolia*, *Carex aquatilis*, and *Eriophorum angustifolium*.

Secondary plant succession on tundra mudflows on silty soil was described by Lambert (1972). In that Canadian study, two stages of succession were recognized: initially grasses, sedges, and forbs colonized recently exposed silts. After the silts became stabilized, climax species began occupying the site. Pioneer plants seemed to establish from seed, and the climax species developed vegetatively from clumps of the original vegetation which survived the disturbance. The second stage of succession (vegetative spreading by climax species) in the Canadian study resembled that observed by Pegau (1970) in western Alaska.

Morrissey (1979) listed two types of plant succession occurring on drained lake basins in the Alaska Coastal Plain Province. One results from the rapid draining of a lake. Under those conditions, meadow communities gradually occupy the basin. However, if the lake level declines slowly, marsh communities, often dominated by *Arctophila fulva*, *Carex aquatilis*, and other emergent plants, develop in the shallow waters and on recently exposed shelves.

Bliss and Cantlon's (1957), Spetzman's (1959), Lam-

bert's (1972), and Morrissey's (1979) descriptions of natural succession did not focus on sites that had been affected by petroleum or mining developments in either the coastal plain or foothills of Alaska's arctic tundra. Soil developmental stage and/or remnants of climax vegetation largely determined whether primary or secondary plant succession predominated at a given location in those reports. The species composition and time frames of primary and secondary successional sequences would most likely differ. Without knowledge of plants involved, predicting recovery potentials from field observations would be at best perplexing.

Opportunistic and adventive plants in the North American Arctic have not received much attention until recent years. Spetzman (1959) may have been one of the first to specifically document plants occupying that niche on the North Slope of Alaska. A number of such plants have been reported in the USSR Arctic, according to Dorogostaiskaya (as cited by Hernandez, 1973). Because current sources of information provided few details related to succession on the Coastal Plain Province where petroleum developments are occurring, it became obvious that site-specific studies were in order.

Commencing in the early 1970s, experiments with planting techniques, seed treatments, grass species and varieties, soil fertilization, and transplanting local vegetation were conducted in the Prudhoe Bay vicinity and elsewhere on the Alaska North Slope by the University of Alaska's Agricultural Experiment Station (Mitchell et al., 1974; McKendrick et al., 1980). Most of these experiments occurred on drastically disturbed soils. A few experiments were designed to investigate plant colonization on gravel. Some work occurred on accidental and experimental oil spill sites. Establishing permanently marked photoplots was one phase of the Alaska studies aimed at documenting long-term changes in plant communities on disturbances (McKendrick, 1976). Monitoring of photoplots and fertilizer effects has continued to the present. However, comprehensive planting and species screening studies ended after 3 yr.

The seeding experiments produced information as to which indigenous and introduced grass species were feasible for revegetation projects in the Prudhoe Bay vicinity. The purpose was to identify arctic-adapted grasses that could be grown on croplands to produce seed for use in the Arctic. Arctared fescue, a variety of *Festuca rubra*, the origin of which is suspected to be Alaska, has the capacity to establish on mesic sites on the coastal plain as well as in the foothills. Two indigenous grass species that proved well adapted to mesic and relatively dry sites and which could be grown in seed-production operations beyond the Arctic were *Poa glauca* and *Arctagrostis latifolia*. These selections were released and produced commercially (Mitchell, 1979, 1980).

Fertilizer experiments indicated soils at Prudhoe Bay were deficient in available phosphorus. A single application of triple superphosphate fertilizer successfully overcame that deficiency and stimulated rapid reinvasion of mosses, liverworts, and vascular plants on oil-damaged

wet tundra (McKendrick and Mitchell, 1978). Without phosphorus fertilization, revegetation has been slow and poor. Increased available soil phosphorus was also necessary for establishing grass seedlings on physically disturbed soils. Without added phosphorus seeded grasses simply failed to develop plants on most plots.

Recently, research has begun on revegetation and natural succession on both dry (gravel) and wet habitats. A survey of plants colonizing abandoned drilling pads (usually dry habitats) in the National Petroleum Reserve in Alaska (NPR) was conducted in July 1984.

In 1985, a study of the ecological conditions of aquatic and terrestrial sites occupied by *Arctophila fulva* and the life history of the grass was begun. It was a joint effort

among the University of Alaska, Fairbanks, Agricultural and Forestry Experiment Station, the Standard Alaska Production Company (formerly SOHIO), and the U.S. Fish and Wildlife Service. Uncertainties of how to mitigate wetland habitat losses resulting from construction activities prompted the study.

These studies have provided both a spatial and temporal perspective of plant colonization, on man-caused disturbances in Arctic Alaska. This report contains observations and data for plant colonization from three types of disturbances: (1) oil-damaged wet tundra, (2) an abandoned silt road in the Prudhoe Bay vicinity, and (3) 12 exploratory-well drilling pads on an array of locations and substrates in NPR.

STUDY SITES AND METHODS

Substrate (soil) conditions were variable among these studies. For the oil spill, the peaty, silt loam soil profile was largely intact but chemically altered. On the abandoned road, peaty, silt loam soil was physically disturbed but not chemically altered. The road surface was elevated above the surrounding terrain perhaps a meter or more. Drilling pads in NPR included two designs, "thin" and "thick." Thin pads were constructed from materials excavated from the reserve pits. The pad materials often consisted of ice-rich silts and clays, some of which were saline, owing to their marine origins. Thick pads were built by covering the materials excavated from the reserve pit with about one-meter thickness of borrow material from relatively dry locations, often several kilometers from the wellsite, which consisted of either dune or ancient beach sands and fluvial gravels. Often these substrates contained few fine-textured (silt and clay) fractions, and the surfaces of the thick pads were elevated above surrounding terrain about 1.5 m.

RECOLONIZATION OF A SEEDED AND FERTILIZED WET TUNDRA DAMAGED BY CRUDE OIL SPILLAGE

This study was a continuation of observations and measurements on a set of 16 fertilizer (nitrogen, phosphorus, potassium, and magnesium) plots established and seeded to arctic alkaligrass (*Puccinellia borealis*) in early September 1974 near the ARCO (Atlantic Richfield Company) Base Camp at Prudhoe Bay. The design and treatments have been described earlier (McKendrick and Mitchell, 1978). These included seeding with *Puccinellia borealis* and fertilization with individual and combined levels of nitrogen, potassium, phosphorus, and magnesium. Observations of the seeded grass indicated establishment occurred only where phosphorus fertilizer had been applied. The damaged area was essentially devoid of live plants, except for the *Puccinellia* seedlings, from 1975 through 1977. After 1977, plots were not closely examined until August of 1984. It was then discovered that the seeded grass had entirely disappeared, and indigenous graminoids had invaded the phosphorus-fertilized plots. These indigenous plants have now spread vegeta-

tively 30 to 50 cm beyond the original plot borders in some instances.

Canopy cover data by plant species were obtained on 25 July 1985. Three groups of 10 points were read in each plot. A metal frame containing 10 holes drilled to accommodate a steel pin was placed systematically at three locations, for a total of 30 pin positions in each plot. The pin was dropped through the guide holes in the frame to measure vertical projections of the ground cover. Each pin-point encounter with plant material was recorded by species to give an estimate of canopy cover. Basal and bare soil hits were also recorded to measure basal and litter cover.

PHOSPHORUS, POTASSIUM, AND SULFUR FERTILIZATION AT PRUDHOE BAY

This fertilizer experiment was conducted on a mesic/dry silt-loam road surface abandoned in the summer of 1969. The substrate consisted of the typical alkaline (pH about 7.6) silty loam from which soils in the vicinity developed. The road was used during May 1968 to move drilling equipment from the ARCO discovery well to the confirmation well location. The road was constructed by blading soil from the edges to create an elevated surface between the two ditches. This type of construction has been commonly used in temperate zones throughout the United States, but it proved unacceptable in the Arctic, where subsurface ice masses occur. The construction method was abandoned in the Alaska Arctic beginning about 1969.

The study location is near ARCO's Drill Site Number 5 and consisted of two blocks of a randomized complete block design. One block (replicate) was situated in a generally low, relatively mesic section of the road, and the other was located on a more elevated section where soils were relatively dry. The rectangular plots were 1.2 by 1.8 m. Within blocks, the plots were located side by side in a row along the northeast edge of the road. Plot corners were marked with wooden stakes. Loss-on-ignition tests from five randomly selected soil samples of the upper 15 cm of each soil indicated the mesic block soils aver-

aged 19 g organic matter per 100 g of dry soil, and the dry block soils contained 15 g per 100 g of dry soil.

The design was a 2 by 3 by 3 factorial. Variable factors were two replicates and three levels of each of three fertilizers at all possible combinations (54 plots total). Elemental treatment levels were 0, 145, and 290 kg phosphorus ha⁻¹, 0, 89, and 178 kg potassium ha⁻¹, and 0, 28, and 57 kg sulfur ha⁻¹. The phosphorus, potassium, and sulfur sources were triple superphosphate, muriate of potash, and gypsum. These plots were planted to barley (*Hordeum vulgare*) in 1973 to measure plant responses to soil fertilization. The barley lived only 1 yr, and no other species were seeded on these plots.

From 29 August 1973 until 23 July 1985 the plots were not disturbed by man, although geese, caribou, and other wildlife had access to the area. On the latter date, naturally occurring vegetation cover was measured in each plot by the point method described above. Basal hits, vascular plants, bare ground, moss, and liverworts were recorded. These data were then analyzed to determine significance of fertilizer treatments on subsequent natural colonization by indigenous species.

RESULTS AND DISCUSSION

RECOLONIZATION OF A SEEDED AND FERTILIZED WET TUNDRA DAMAGED BY CRUDE OIL SPILLAGE

The test of nitrogen, phosphorus, potassium, and magnesium nutrient additions to this oil-damaged habitat indicated phosphorus and potassium had positively influenced vegetation recovery. Nitrogen and magnesium produced no observed impact alone although nitrogen enhanced plant responses to phosphorus applications (McKendrick and Mitchell, 1978). These findings contrast with observations by Hutchinson and Freedman (1975), who indicated fertilization with nitrogen and phosphorus was ineffective in promoting plant growth on oil-damaged sites, primarily because living plants were absent in their

PLANT COLONIZERS ON ABANDONED DRILLING PADS

During early July 1984, 12 wellsites in the NPRA (Table 1) were visited and the vascular plant species observed on the drilling pads were listed. Patterns in these data indicated which species were the ones most frequently colonizing the disturbances and differences in regional revegetation potentials. Furthermore, they showed which of the seeded grasses were useful for establishing plant cover.

All of the pads had been seeded and fertilized (nitrogen, phosphorus, potassium) one to several times (McKendrick, 1986). Substrates varied from gravel and sand to sandy silts with variable amounts of organic material. The construction objective was to obtain ice-free fill materials for the thick, all-season pads and those materials were either borrowed from dry ridges or excavated at the wellsites. The nearest source was selected to keep hauling to a minimum. Soil reactions ranged from alkaline to acidic in the surrounding undisturbed areas. Some soils on thin pads near the coast were saline (McKendrick, 1986).

In our study, there was less bare ground and more litter in plots receiving either of these two nutrients (Table 2). Of the two nutrients, phosphorus was substantially more influential than potassium.

Moss cover was visibly increased by phosphorus fertilization. The effects were sufficient to insulate the soil and reduce annual thaw depths. These are the first experimental plots where I have been able to measure a reduction in annual thaw depth caused by revegetation. Plant biomass, primarily mosses, insulate the soils in this region and restrict the annual depth of thaw. Where soil moisture holding capacities are sufficient, subsurface ice lenses accumulate, elevating the surface of the terrain. If the

TABLE 1

Location and drilling chronology data for twelve exploratory wellsites in the National Petroleum Reserve in Alaska^a

Wellsite	Year(s) drilled	Year(s) seeded	Elevation (m)	Location		Pad construction material
				Latitude N	Longitude W	
Inigok No. 1	1978-79	1980, 82	23	70°00' 17.48"	153°05' 56.91"	Sandy gravel
South Meade No. 1	1978-79	1979, 80, 82	11	70°36' 53.92"	156°53' 23.60"	Sand
Awuna No. 1	1981	1981, 82	335	69°09' 11.58"	158°01' 21.27"	Silt
Peard No. 1	1979	1979, 80, 82	21	70°42' 56.32"	159°00' 02.51"	Silt and clay
Tunalik No. 1	1978-80	1980, 82	24	70°12' 21.45"	161°04' 09.15"	Silt, sand and gravel
Seabee No. 1	1979-80	1981, 82	88	69°22' 48.51"	152°10' 31.29"	Sandy gravel
Lisburne No. 1	1979-80	1981, 82	559	68°29' 05.43"	155°44' 35.51"	Sand and gravel
Kugrua No. 1	1978	1979, 80, 82	18	70°35' 13.28"	158°39' 43.25"	Silty sand
East Teshekpuk No. 1	1976	1978	2	70°34' 11.66"	152°45' 35.90"	Fine sand
Ikpikpuk No. 1	1978-80	1980	10	70°27' 19.66"	154°19' 52.78"	Silty sand
East Barrow No. 17	1978-79	1979, 80	2	71°14' 00.45"	156°16' 34.32"	Beach sand
East Barrow No. 20	1980	1980	2	71°13' 57.02"	156°20' 11.98"	Beach sand

^aDrilling pads at these wellsites were examined during July 1984.

thermal conductivity of the soil is altered by removing vegetation, and thaw-depths increase, the ice masses melt and the terrain subsides. Artificial revegetation goals in the Prudhoe Bay vicinity were originally aimed at restraining active layer thaw and restoring the former thermal equilibrium.

At times, the polygon basin in which these plots were located contained standing water 2 to 3 cm in depth. By 1984, each phosphorus-fertilized plot was elevated above the water surface, presenting a striking contrast with the unfertilized surroundings and adjacent plots not receiving phosphorus. On 5 August 1987, thaw depths averaged 42.9 (standard error = 0.27) and 45.8 (standard error = 0.21) cm, respectively, in the phosphorus and nonphosphorus plots.

In addition to being elevated and having a fairly uniform moss cover, these phosphorus-fertilized locations also supported vigorous specimens of two indigenous perennial graminoids, *Carex aquatilis* and *Dupontia fisheri*. In 1985, there was only one *Puccinellia borealis* plant remaining from the eight small stands established 10 yr earlier. No other species of vascular plants have invaded these plots by August 1987. *Carex aquatilis* was the most common vascular plant found surviving in sites affected by reserve pit leaks in the National Petroleum Reserve in Alaska (McKendrick, 1986). *Dupontia fisheri* also survived reserve pit fluid leaks but was not found as often as was *Carex aquatilis*, possibly because this grass is not distributed as consistently throughout the region as is the sedge. The timing of when *Puccinellia* died and *Carex* and *Dupontia* recolonized cannot be reported, because there were no opportunities to observe the site between 1977 and 1984. The changes in species dominance occurred during the 7-yr period as the seeding's age advanced from 3 to 10. Litter from the *Puccinellia* plants was sparse in 1984, suggesting that species had not grown on the plots for several seasons. Flooding is believed to be at least partially responsible for the dying of *Puccinellia*, a plant that occurs naturally on well-drained habitats in the region.

Colonization by *Carex* and *Dupontia* (both rhizomatous) occurred either as seedlings and/or from rhizome buds that survived the crude oil damages. We were unable to determine which occurred in this study. We are certain the recolonization was not from a vegetative encroachment from the edges of the spill, because a barren zone separated our plots from the surrounding vegetation.

There are literature accounts and circumstantial evidence supporting both vegetative and sexual forms of reproduction during recolonization in the Arctic. In a physically disturbed site, *Carex bigelowii*, a tufted sedge, clearly invaded as seedlings in vehicle tracks and in a corral on a tussock tundra site near Unalakleet (McKendrick, 1981). Roach (1983) reported significant quantities of buried seed in northern Alaska tundra soils. McGraw (1980) and Gartner et al. (1983) concluded buried seed was a major factor affecting revegetation of denuded tussock tundra. The buried seed of *Carex bigelowii* and *Eriophorum vaginatum* were in the organic horizon of soils

examined in those two studies. The organic horizon was intact in our wet-tundra oil-spill plots and perhaps some seeds survived damage from the crude oil. If there were buds surviving, they produced no aboveground evidence of their existence for several growing seasons following the spill. However, *Carex aquatilis* can tolerate a degree of crude oil damage from drilling wastes (McKendrick, 1986). Diesel and JP-4 are notably more toxic to plants than crude oil. Perhaps that ability coupled with that of the phosphorus fertilizer application was enough to encourage that sedge's vegetative recovery.

Dupontia was distributed less uniformly than *Carex* among the plots, indicating the colonies may have originated from only one or two clones (seedlings?). Lawson et al. (1978) reported that natural recolonization of plants

TABLE 2
Mean cover data and analysis of variance F-test probabilities (n = 16) for bare ground, litter, standing dead, moss, and two graminoids in plots treated with four fertilizers^a

Nutrient	Cover (%)		F-test significance
	Unfertilized	Fertilized	
	Bare Ground		
N	51	48	.19
P	77	15	.01
K	53	46	.10
Mg	54	46	.45
	Litter		
N	12	12	.91
P	5	21	.05
K	9	17	.09
Mg	10	15	.44
	Standing Dead		
N	21	11	.15
P	4	33	.05
K	12	22	.14
Mg	10	23	.14
	Moss		
N	38	45	.65
P	17	71	.00
K	38	45	.65
Mg	33	48	.32
	<i>Carex aquatilis</i>		
N	18	10	.09
P	4	27	.03
K	12	17	.16
Mg	13	16	.56
	<i>Dupontia fisheri</i>		
N	3	5	.32
P	1	7	.12
K	4	3	.53
Mg	3	5	.50

^aFourteen growing seasons had lapsed since the spill occurred. Fertilizer had been in place for 11 growing seasons. Cover data were collected 25 July 1985. *Dupontia* and *Carex* were the only vascular species on these plots.

on the coastal plain varied from slight to complete in their responses to crude oil spills at the Fish Creek Wellsite. Walker et al. (1978) observed that *Carex* spp., *Eriophorum* spp., and *Salix* spp. were the three genera that seemed most tolerant of oil spills, after a year of exposure to crude and diesel oils in experimental spills in the Prudhoe Bay vicinity.

Our study plots have a relatively long history (15 yr at this time) of vegetation observations on an accidental crude oil spill in the Prudhoe Bay region. Continued monitoring of these test plots and vegetation changes will undoubtedly prove interesting and useful in an applied ecological sense.

PHOSPHORUS, POTASSIUM, AND SULFUR FERTILIZATION AT PRUDHOE BAY

In the vicinity of this study, five forb, nine graminoid, and two shrub species were most frequently observed colonizing the abandoned road's surface in 1985, 17 growing seasons after the soil was disturbed. Forbs included *Braya purpurascens*, *Draba* spp., *Eutrema edwardsii*, *Equisetum variegatum*, and *Melandrium apetalum*. *Salix arctica* and *S. fuscescens* were the two shrub species. Graminoids included *Alopecurus alpinus*, *Carex aquatilis*, *Deschampsia caespitosa*, *Dupontia fisheri*, *Festuca baffinensis*, *F. brachyphylla*, *F. rubra*, *Poa glauca*, and *Puccinellia arctica*. Correlation coefficient data for the prominent species are presented. The most significant correlation coefficients are shown in Table 3. Moss, liverwort, and vascular plant occurrences all showed clearly that phosphorus fertilization encouraged colonization of these plants. In contrast, there was a definite correlation between bare ground and the absence of phosphorus fertilization.

Braya purpurascens was negatively related to phosphorus fertilization and standing dead and litter. Readers are cautioned against interpreting these data as an indication that *Braya* is intolerant of phosphorus fertilization. These data for 1985 represent conditions 17 yr after the disturbance and do not characterize the previous pattern of plant invasion. *Braya* specimens in the phosphorus fertilized plots were more vigorous than their unfertilized counterparts during the initial colonization stages.

Braya was the first genus to invade the road surface by seedling establishment, four to five years after the road was constructed. Original plants on the road were sparse and about 8 to 12 cm in height. During subsequent years, monospecific stands of *Braya* became quite prominent in certain locations, particularly where soils were mesic to moist. Subsequently, seedlings of graminoids and other forbs began preferentially invading the phosphorus fertilized plots, and soon out-competed the *Braya*. Ten to 12 yr after fertilizing, only the unfertilized plots remained relatively free of competition for *Braya*. Apparently, *Braya* is more adapted to surviving on the phosphorus-poor soils than the other plant species colonizing. This forb does not seem to be a strong competitor with either rhizomatous or tufted grasses. It persists on relatively dry sites in a low-growing and diminutive form.

Potassium and sulfur fertilization had no apparent influences benefiting recolonization at this study location. Cover values for phosphorus-fertilized plots are shown in Table 4. Total plant and litter cover was about 1.6 times greater on the phosphorus-fertilized plots. There appeared to be no advantage in increasing fertilizer beyond the first application level. In other fertilizer tests at Prudhoe Bay, we have observed no significant plant responses to phosphorus applications greater than 45 kg ha⁻¹. In a current test with *Arctophila fulva* transplants, we have obtained a linear increase in shoot densities among fertilizer application rates of 0, 15, and 30 kg P ha⁻¹. Based on those results, applying approximately 50 kg P ha⁻¹ in this experiment on the abandoned road would most likely have produced results comparable to those of 145 kg ha⁻¹.

Lack of differences in litter and standing dead among phosphorus-fertilizer levels shown in Table 4 suggests that, after 13 yr, *Braya* and other species occurring primarily on the plots not treated with phosphorus produced residue comparable to that of other species on the phosphorus-treated plots. Litter and standing dead were distributed differently between phosphorus and nonphosphorus plots. The biomass of litter and standing dead was clumped, and standing dead was taller on the phosphorus-fertilized plots, where tufted graminoids predominated. That has benefits favoring recolonization, especially on elevated surfaces where snow cover is likely to be removed by wind.

Pioneering by *Braya* seemed to favor the subsequent colonization of other plants, but that is only one of perhaps many interspecies relationships occurring during succession at this location. A rather obvious benefit to *Braya* plants accrued from both seeded and naturally invading grasses in the form of wind protection. The erect display of standing dead produced by the grasses is a wind break superior to that of more prostrate growth forms. The standing dead grass captures snow to the depths of those plants' heights. Some relationships between vegetation

TABLE 3
Cover and fertilizer treatment correlation coefficients (n = 54) for the most significant point data from plots on an abandoned silt road at Prudhoe Bay, Alaska, 13 growing seasons following fertilization

Variable 1	Variable 2	r	Two-tailed probability
Liverwort cover	Vascular plant and moss ^a	.75	(.000)
Moss cover	P-fertilization	.54	(.001)
Bare ground	P-fertilization	-.51	(.000)
<i>Braya purpurascens</i>	P-fertilization	-.40	(.001)
<i>Braya purpurascens</i>	Standing dead and litter	-.44	(.000)

^aHits for live vascular plants and moss were combined to form a single variable.

and snow cover have been studied on the Seward Peninsula by Brooks and Collins (1984). Primarily *Braya*, but some other species, formed flourishing colonies in the micro-sites on the leeward side of seeded grass plots on this road surface. Effects of wind eroding the soil surface were quite evident at the edges of the grass colonies.

Willow colonizers were limited in species and sparse at Prudhoe Bay sites. *Salix arctica* and *S. fuscescens* were the two commonly noted. Neither *Salix alaxensis*, which predominated in Bliss and Cantlon's (1957) study, nor *Salix pulchra* ssp. *pulchra*, which was most frequently found on drilling pads in NRPA (discussed below), occurred on the road disturbances at Prudhoe Bay; both species are rare in the undisturbed surroundings. *Salix planifolia* ssp. *pulchra* seems to be replaced by *Salix lanata* ssp. *richardsonii* in undisturbed communities on alkaline soils at Prudhoe Bay, occurring in only certain habitats. However, *Salix lanata* ssp. *richardsonii* was not frequently found pioneering man-caused disturbances in that locality. *Salix alaxensis* occurs along river courses and is apparently unadapted to the general terrestrial sites in the area.

IDENTIFYING PLANT COLONIZERS ON ABANDONED DRILLING PADS AND SITES AFFECTED BY RESERVE PIT FLUIDS

Vegetation on the pads included indigenous plants and seeded species. At certain locations on the Coastal Plain Province, the impacts from grazing geese and caribou were clearly sufficient to prevent seeded grass stands from persisting.

Thirty-six forbs, 30 graminoids, and 7 shrubs were recorded on drilling pads in the NPRA (Table 5). Forbs most frequently invading were *Senecio congestus*, *Artemisia tilesii*, and *Cochlearia officinalis*. Readers are reminded that the survey was of exploratory drilling pads which were not located to proportionately represent the habitats of either the NPRA or the North Slope. Only three of the wellsites were in foothill locations. Observations indicated forbs began invading abandoned drilling pads soon after pads were constructed, and there are forb species in the region with a propensity for such a role in succession. Hernandez (1973) reported *Senecio congestus* was one forb inclined to invade wet and mesic habitats in his seismic line studies. Lambert (1972) observed this *Senecio* species was one of the pioneers on exposed silty

TABLE 4
Percent cover means (standard error) for point data collected
23 July 1985 from phosphorus-fertilized soils on a road at
Prudhoe Bay after it had been abandoned for 15 yr^a

Cover component	P-fertilizer applications (kg ha ⁻¹)		
	0	145	290
Bare ground	38.7 (3.8)	11.1 (2.8)	14.8 (4.0)
Dead organic matter			
Animal dung	0.2 (0.2)	0.6 (0.4)	0.4 (0.3)
Litter and standing dead	32.7 (2.8)	42.5 (4.6)	36.4 (5.5)
Cryptograms			
Liverwort	1.3 (0.5)	7.4 (3.6)	6.1 (3.3)
Moss	36.1 (4.4)	65.1 (3.4)	64.0 (4.1)
Forbs			
<i>Braya purpurascens</i>	21.8 (2.4)	13.8 (0.7)	11.4 (2.4)
<i>Equisetum variegatum</i>	0.0	0.0	0.4 (0.4)
<i>Eutrema edwardsii</i>	0.4 (0.3)	0.2 (0.2)	0.0
Graminoids			
<i>Alopecurus alpinus</i>	0.7 (0.6)	7.0 (2.9)	5.2 (2.9)
<i>Carex aquatilis</i>	0.7 (0.6)	3.1 (1.1)	3.5 (1.6)
<i>Deschampsia caespitosa</i>	0.6 (0.4)	1.1 (0.5)	1.8 (1.0)
<i>Dupontia fisheri</i>	0.0	1.3 (1.1)	0.4 (0.4)
<i>Festuca baffinensis</i>	0.0	4.6 (1.8)	2.2 (2.2)
<i>Festuca rubra</i>	0.6 (0.6)	1.7 (1.0)	1.5 (1.0)
" <i>Festuca vivipara</i> "	0.6 (0.6)	1.5 (1.5)	0.0
<i>Puccinellia arctica</i> ^b	2.4 (1.2)	4.6 (2.1)	4.1 (2.2)
Shrubs			
<i>Salix arctica</i>	0.0	0.9 (0.9)	0.2 (0.2)
<i>Salix fuscescens</i>	0.7 (0.4)	0.9 (0.5)	0.7 (0.3)
Mean live canopy cover	65.9	113.2	101.5

^aFertilizer was applied once, 13 years before these measurements were taken, and plants established naturally.

^bComplex recognized by Welsh (1974) containing *Puccinellia borealis*.

TABLE 5
 Listing of vascular plant species colonizing abandoned drilling pads at ten coastal plain and two foothill exploratory wellsites
 in the National Petroleum Reserve in Alaska

Plant species	Coastal Plain Wellsites									Foothill Wellsites			Total wellsites
	East Barrow No. 17	East Barrow No. 20	Peard No. 1	South Meade No. 1	Kugrua No. 1	Teshekepkuk No. 1	Ikpikpuk No. 1	Inigok No. 1	Tunalik No. 1	Seabee No. 1	Awuna No. 1	Lisburne No. 1	
Forbs													
<i>Achillea borealis</i>										X			1
<i>Aconitum delphinifolium</i> subsp. <i>paradoxum</i>												X	1
<i>Androsace septentrionalis</i>												X	1
<i>Arabis lyrata</i>						X		X					1
<i>Artemisia alaskana</i>					X	X				X			3
<i>Artemisia borealis</i>				X						X		X	3
<i>Artemisia tilesii</i>				X	X				X	X		X	5
<i>Aster sibericus</i>												X	1
<i>Astragalus alpinus</i> subsp. <i>alpinus</i>										X		X	2
<i>Astragalus alpinus</i> subsp. <i>arcticus</i>					X							X	2
<i>Cerastrium beeringianum</i> var. <i>beeringianum</i>												X	1
<i>Cochlearia officinalis</i>	X	X	X						X				4
<i>Chrysanthemum bipinnatum</i>					X								1
<i>Chrysosplenium tetrandrum</i>					X							X	2
<i>Descurainia sophioides</i>										X	X	X	3
<i>Draba cinerea</i>								X					1
<i>Draba lactea</i>								X					1
<i>Epilobium angustifolium</i> *									X				1
<i>Epilobium latifolium</i>										X		X	2
<i>Equisetum arvense</i>										X		X	2
<i>Oxytropis campestris</i> subsp. <i>gracilis</i>												X	1
<i>Oxytropis</i> spp.								X					1
<i>Oxytropis vicida</i>												X	1
<i>Papaver lapponicum</i> subsp. <i>porsildii</i>												X	1
<i>Petasites frigidus</i>											X		1
<i>Polemonium acutiflorum</i>										X		X	2
<i>Polygonum viviparum</i>												X	1
<i>Ranunculus gmelinii</i> subsp. <i>gmelinii</i>											X		1
<i>Ranunculus hyperboreus</i> subsp. <i>hyperboreus</i>												X	1
<i>Rumex arcticus</i>					X						X		2
<i>Sagina intermedia</i>					X								1
<i>Saxifraga cernua</i>											X	X	2
<i>Senecio congestus</i>				X		X	X	X	X	X	X		6
<i>Stellaria crassifolia</i>											X		1
<i>Stellaria edwardsii</i>												X	1
<i>Stellaria longipes</i>										X			1
Total forb species	1	1	1	3	7	2	5	0	4	11	7	20	
Graminoids, Grasses													
<i>Agropyron boreale</i> ssp. <i>alaskanum</i>												X	1
<i>Agropyron macrourum</i>										X			1
<i>Alopecurus alpinus</i>		X	X			X			X				4
<i>Arctagrostis latifolia</i>				X		X	X	X	X	X	X	X	8
<i>Arctophila fulva</i>			X		X	X	X		X				5
<i>Bromus pumpellianus</i>										X			1
<i>Calamagrostis holmii</i>	X									X			2
<i>Deschampsia caespitosa</i>				X									1
<i>Deschampsia caespitosa</i> subsp. <i>orientalis</i>							X						1
<i>Dupontia fisheri</i>						X			X				2
<i>Elymus arenarius</i>				X									1
<i>Festuca baffinensis</i>												X	1
<i>Festuca brachyphylla</i>						X							1
<i>Festuca ovina</i> var. <i>brevifolia</i>	X												1
<i>Festuca rubra</i>				X		X	X	X	X	X	X	X	8
<i>Hierochloe alpina</i>											X		1
<i>Phippsia algida</i>	X	X			X				X				4
<i>Poa arctica</i>									X	X		X	3
<i>Poa glauca</i>	X		X		X		X	X	X	X		X	8
<i>Poa pratensis</i>							X						1
<i>Poa pseudoabbreviata</i>				X									1
<i>Trisetum spicatum</i>												X	1
Total grass species	4	2	3	5	3	6	6	4	11	7	5	17	
Sedges and Rushes													
<i>Carex aquatilis</i>								X	X				2

TABLE 5 (cont.)

Plant species	Coastal Plain Wellsites									Foothill Wellsites			Total wellsites
	East Barrow No. 17	East Barrow No. 20	Peard No. 1	South Meade No. 1	Kugrua No. 1	Teshekekuk No. 1	Ikpikpuk No. 1	Inigok No. 1	Tunalik No. 1	Seabee No. 1	Awuna No. 1	Lisburne No. 1	
<i>Carex bigelowii</i>												X	1
<i>Eriophorum angustifolium</i>											X		1
<i>Eriophorum vaginatum</i>									X				1
<i>Juncus arcticus</i>											X		1
<i>Juncus castaneus</i> ssp. <i>castaneus</i>												X	1
<i>Luzula arcuata</i> subsp. <i>unalaschensis</i>												X	1
<i>Luzula wahlenbergii</i>									X				1
Total sedge and rush species	0	0	0	0	0	0	0	1	3	0	2	3	
Shrubs													
<i>Rubus chamaemorus</i>											X		1
<i>Salix alaxensis</i>										X		X	2
<i>Salix brachycarpa</i> ssp. <i>niphoclada</i>										X			1
<i>Salix fuscescens</i>											X		1
<i>Salix lanata</i> ssp. <i>richardsonii</i>											X		1
<i>Salix phlebophylla</i>											X		1
<i>Salix plantifolia</i> ssp. <i>pulchra</i>					X					X	X	X	4
Total shrub species	0	0	0	0	1	0	0	0	0	3	5	2	
Total vascular plant species	5	3	4	8	10	8	11	5	18	21	19	32	

*This species was probably introduced with grass seed. Only one specimen was found, and it was deformed and not growing well in this habitat.

soil where moisture seepages exist. I noticed *Senecio* colonizing moist and mesic habitats on the drilling pads in NPRA. Furthermore, it appeared capable of invading several substrates that differed in texture. It was not found on the Lisburne No. 1 drilling pad, which had the highest diversity of forb species. At Umiat, near the location of the Seabee No. 1 exploratory wellsite, Spetzman (1959) reported *Senecio congestus* increased from a couple of plants to a dense weedy growth along the gravel airstrip in a 3-yr period (1947 to 1950). In August 1987, I observed a similar invasion of robust *Senecio congestus* in a wet basin along the northern edge of the Franklin Bluffs Construction Camp Pad, and I have seen the plant on pads in the Prudhoe Bay vicinity. This plant is also an opportunist in Alaska's interior habitats, colonizing agricultural clearings (Conn and DeLapp, 1983).

Artemisia tilesii occurred on drilling pads in both the Coastal Plain Province and the Brooks Range Foothills, and this is one of the common species in the "perennial herb" communities described by Bliss and Cantlon (1957). In contrast, *Cochlearia officinalis* was confined to coastal locations. Spetzman (1959) noted *Cochlearia officinalis* was one of four common invaders in disturbances around the Barrow village.

Diversity of colonizing species was clearly greater away from the coastal habitats, reaching its zenith in the foothills (Table 5). That was due to not only a greater plant species diversity in surrounding undisturbed habitats away from the coast, but also to greater seed production by plants influenced less with the marine environment. The greater diversity among plant species occurred on drilling pads producing notably sparse vegetation. I have also noted similar responses along the Trans-Alaska Pipeline route. Where seeded grasses are dense, natural invasion is limited in species diversity and numbers of individuals.

Three other forbs occurred on one-fourth of the drilling pads: *Artemisia alaskana*, *A. borealis*, and *Descurainia sophioides*. Of these, *Descurainia* appeared to be confined to the inland locations, while the other two were more widely distributed. These two *Artemisia* species were among those colonizing river alluvium along the Colville River (Bliss and Cantlon, 1957). Except for the *Artemisia* species, few forbs found in the Colville River study were also common in this drilling pad survey. *Descurainia*, *Senecio*, and *Androsace septentrionalis* were the only biennial colonizing species found in this survey. Of these three species, *Senecio congestus* produces seeds most easily transported by wind, which may explain its wide distribution and frequent occurrences on disturbed ground in the Arctic.

Of the graminoids, grasses were the most prominent invaders of drilling pads. Two-thirds of the pads evaluated were variously occupied by *Arctagrostis latifolia*, *Festuca rubra*, and *Poa glauca*. *Festuca rubra* was consistently included in each seed mixture used on these pads. It is fairly well suited to a variety of habitats in the Arctic. According to Hultén (1968), this species is widely distributed throughout the region.

Arctagrostis latifolia and *Poa glauca* were also included in seed mixtures applied to the drilling pads when these seeds could be obtained. These two grasses were being grown for seed production in south-central and interior Alaska, but the supply was inconsistent among years during the NPRA drilling-pad rehabilitation program. Both species occur widely in the Alaska Arctic. One grass included in all seeding mixtures that consistently failed was *Poa pratensis* variety "Nugget." This grass is not well adapted to the Arctic environment and persists only as small clumps in protected microhabitats.

Heavy grazing by geese and caribou seemed to be a detrimental factor for seeded grasses in certain of the

coastal plain localities. Geese and caribou preferentially graze seedlings of *Poa pratensis*. The grazing pressures were heaviest where molting occurred, such as at the Peard location (McKendrick, 1986). At such sites, colonization by vascular plants was either absent or restricted to salt-tolerant species, i.e., *Phippisia algida* and *Puccinellia* spp. Caribou also grazed seeded grasses excessively on some pads. Excessive grazing of seedlings was very likely responsible for seeding declines in vigor.

Arctophila fulva was found on five of the 12 drilling pads in this survey. Spetzman (1959) listed the habitats for this grass as "silty- or sandy-bottomed lakes, or slowly moving streams; brackish coastal wet meadows; in water up to 4 ft deep or wet soil." Finding it colonizing on elevated and relatively dry sites was unexpected. Others have reported that this grass invades disturbances that are wet, colonizing lake basins and similar sites (Britton, 1957; Bliss and Wein, 1972a, 1972b; Hernandez, 1973; Morrissey, 1979; Billings and Peterson, 1980; Everett, 1980). The occurrences of *Arctophila fulva* on drilling pads was confined to the Coastal Plain Province (Table 5), in the NPRA survey. Subsequently, I have found *Arctophila fulva* colonizing gravel habitats in material sites and on the work pad along the Trans-Alaska Pipeline route in the foothills region. There may be a significant relationship with migratory waterfowl and the colonization by this grass.

Exactly how the propagules of *Arctophila* are moved about by grazers is unclear. Speculations that birds moved the grass to new locations has been suggested in a Norwegian study (Elven and Johansen, 1981). I hypothesized the influences of artificial revegetation and grazing geese were significant in the distribution of *Arctophila fulva* to new disturbances in this study.

It is not known whether vegetative parts or seeds are actively involved in the process. Both have possibilities. We have successfully germinated *Carex* spp. seed that was present in waterfowl feces near ponds in the Prudhoe Bay oil field. We have not yet found *Arctophila* seeds in waterfowl feces.

Culms of *Arctophila* freely root, and axillary buds on detached shoots in suitable habitats readily develop into new plants. This vegetative reproduction process seems to require consistently moist conditions, such as found at the margins of ponds and streams. The absence of continually moist soil on drilling pads would restrict vegetative introductions to narrow time-frames during the growing season, and would indicate seeds have a better chance of establishing colonies on dry sites. We have not observed *Arctophila* seed production on emergent plants in the Prudhoe Bay area, but we have found seeds that appeared mature on plants in the foothills region.

The supply of available seed is limited both quantitatively and spatially; therefore, a vector that is particularly attracted to *Arctophila* habitats and subsequently to disturbances must carry the seed to new locations. Migratory waterfowl appear as the most likely vectors.

No species of sedge or rush consistently invaded drilling pads. Apparently, seeds of these species were either

unavailable for early colonization of pads, or the environmental conditions of the pads were simply unfavorable for their requirements. This is essentially another interpretation of what Bliss and Cantlon (1957) observed when they noted climax community plants were not components of the pioneering stands in the tussock tundra succession. In contrast, Gartner et al. (1983) found *Carex bigelowii* and *Eriophorum vaginatum* were dominant colonizers in typical tussock tundra soils in the foothills region that had been denuded by blading. Buried seeds of these two species were found in the organic soils of a central Alaska site (McGraw, 1980). The substrate in both of those studies differed substantially from that of the drilling pads contained in NPRA, in that the drilling pads had few if any remnants of the original soil organic horizons and hence little chance of buried seed. Furthermore, the drilling pads were usually substantially better drained than the undisturbed terrain, because they were elevated. Consequently, soil fertility, natural structure, and moisture conditions of the bladed site in the Gartner et al. (1983) study were most likely more favorable to plant colonization than those of drilling pads in NPRA. Locations away from the coast were the sites in which these plants seemed to invade most successfully. Perhaps that was due to seed production being favored in these inland habitats. Spetzman (1959) observed that *Carex aquatilis* was the most common species in the wet sedge meadow communities near Barrow, but little fruiting was noted in his 1949 survey. He speculated that fruiting may occur only during favorable years.

In contrast, Hernandez (1973) listed *Carex aquatilis*, *Eriophorum angustifolium*, *E. vaginatum*, *Luzula confusa*, and *Carex capillaris* as pioneers on various substrates in the Mackenzie Delta, where treeline reaches the coast. Only the last two species were found on dry habitats. The rest preferred either wet or moist locations. Since the drilling pads in the NPRA survey were relatively dry and sometimes, even when they were wet, provided saline habitats (McKendrick, 1986), they may represent conditions poorly suited for most of the sedges and rushes in this region, until site conditions improve.

Drilling pads located in the wet tundra offer an environment much drier and less protected from wind than the undisturbed surroundings. Consequently, plants adapted to successfully invading these pads would most likely come from the most exposed and driest habitats, such as polygon rims, river terraces, etc. In many instances, such habitats are either uncommon or relatively small components of the landscape adjacent to the drilling pads. That limits the availability of plant propagules of pioneering species adapted to the pad environments, and it may delay succession. Once invasion by adapted species begins, the early pioneers may become the primary seed source for the colonization process, as noted previously with *Braya purpurascens* on the abandoned roads at Prudhoe Bay.

This type of succession resembles the early stages described by Bliss and Cantlon (1957) on river alluvium. However, a significant difference in soil formation exists

between a gravel pad and river alluvium. The early stages of succession on the river site are dominated by flooding and deposition of fine materials. Thus allogenic processes dominate the habitat changes and build a layer of mineral soil. Later in the sequence, autogenic (organic matter accumulations) predominate the habitat changes, and species unadapted to the gravel sere begin occupying the site. Pioneer plants are largely missing in the climax stage, and climax species are absent in the pioneer stage.

In contrast to the fluvial environments, drilling pads, especially those constructed from gravel, have no natural opportunity to receive significant inputs of fine-textured material from which a soil profile may be developed. In the absence of such materials, autogenic processes are all that is available to improve the habitat. Hence, from a practical view this is a form of primary succession and progress beyond the early successional stages may not be anticipated on the gravel pads for a very long time, unless

fine-textured materials, capable of moisture retention, are added. The goal of revegetation for such sites must be carefully selected. Because the physical environment has been altered substantially, achieving a plant community similar to the surrounding habitat is unrealistic. Establishing a self-perpetuating vegetation cover, albeit different from the original, is a realistic goal.

Where disturbances result in thermal erosion, the new habitat is often as wet or wetter than the surroundings. Here secondary succession occurs, as soils are already formed. These kinds of disturbances are invaded readily by both seedlings and vegetative propagation from the edges. Vegetative reproduction from plants along the edges of the disturbance often predominates. The source of adapted plant species for these conditions is substantially greater than for the dry disturbances, discussed above. For small disturbances along roads, a complete cover of vascular plants may occur in less than 10 yr.

CONCLUSIONS

Two types of plant succession were observed in these studies: (1) establishment by seedlings, which predominated on dry sites, and (2) vegetative invasion from surrounding communities, which was most common on wet sites.

Where severe crude oil damage occurred to wet-sedge meadow sites, mosses and graminoids returned within 10 to 12 yr under the influence of phosphorus fertilization. Sometime between the third and tenth year, *Carex aquatilis* and *Dupontia fisheri* replaced *Puccinellia borealis*, which had been seeded. By the tenth year, following seeding and fertilizing, the influences of insulation by vegetation were decreasing the thaw depth in the soil. Vegetative and sexual reproduction probably occurred in various proportions on this spill location.

Phosphate was the most effective fertilizer, encouraging natural vegetation on physically disturbed silt loam. *Braya purpurascens* was the dominant forb initially invading those soils at Prudhoe Bay, but it was conspicuously absent in the larger survey in NPRA. Presumably, the alkaline soils at Prudhoe Bay were responsible for that disparity. Graminoids predominated colonization at Prudhoe Bay after initial invasion by *Braya*. These plants provided wind protection that reduced soil erosion, trapped snow, and encouraged establishment of other plants.

Among the 12 locations examined, a total of 73 vascular plant species were found colonizing drilling pads. From 3 to 35 vascular plant species were found colonizing each drilling pad (mostly from seed) within 5 to 8 yr after construction. The largest number of colonizers occurred on gravel drilling pads in the foothills, and the lowest numbers were on coastal plain drilling pads constructed from fine-textured material. Except where salinity of the substrate existed, plant colonization was usually more dense on the thin pads than on the thick pads. Environmental factors promoting vegetation estab-

lishment were growing season conditions favoring seed production in the surrounding vegetation stands and soil properties favoring soil moistness and nutrient availabilities. Site factors believed responsible for poor recolonization were soil dryness, soil salinity, low seed production in surrounding communities, heavy grazing by geese and caribou, and elevation differences that created large dissimilarities between the environments of pad and surrounding landscape. Plants adapted to the overall environments of the pad were often either absent in the surrounding communities or occurred on minor expressions within the local landscape mosaic.

Forbs and tufted grasses dominated pioneering communities where primary succession occurred. Where soil moisture and available nutrients were adequate, liverwort and mosses were often common pioneers during secondary succession. Shrubs and sedges were insignificant colonizers in most sites undergoing primary succession. Rhizomatous graminoids and mosses dominated secondary succession on wet sites.

Arctophila fulva was found colonizing disturbed terrestrial areas as well as disturbances in aquatic habitats. Often these occurrences were in new locations distant from older stands, suggesting a biological vector was responsible for moving the plant to new locations, some of which were undergoing a form of primary succession. Coincidences of heavy grazing by caribou and geese and *Arctophila* colonizations provided a basis for hypothesizing that migratory wildlife might be responsible for introducing the grass to new sites.

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