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Source: *Ecological Applications*, Vol. 7, No. 1 (Feb., 1997), pp. 218-235

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/2269419>

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EFFECTS OF ROADSIDE DISTURBANCE ON SUBSTRATE AND VEGETATION PROPERTIES IN ARCTIC TUNDRA

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Abstract. Tundra adjacent to the gravel Dalton Highway in northern Alaska was examined for effects of 15 yr of chronic road and road dust disturbance. Road effects at a nonacidic site (soil pH ≥ 5.0) and an acidic site (soil pH < 5.0) were compared to examine differential susceptibility. Overall, effects on vegetation were more pronounced in acidic tundra. Initial substrate pH appears to control the degree of response to disturbance by road and calcareous road dust. Soil at the acidic site is normally pH 4.0, whereas in the disturbed area next to the road soil pH was as high as 7.3 ± 0.07 (at 2 m from the road edge). Soils next to the road had lower nutrient levels, altered organic horizon depth, higher bulk density, and lower moisture. Effects on snowpack include both increased drifting in the lee of the road and earlier meltout near the road due to dust-induced change in albedo. Permafrost thaw was deeper next to the road at both sites, and potentially could affect road structure detrimentally. Vegetation biomass of most taxa was reduced near the road at both sites. Total aboveground biomass of nonacidic tundra ranged from 330.0 ± 34.72 g/m² (mean ± 1 SE) at 2 m from the road to 690.7 ± 94.52 g/m² at 100 m away from the road. Total biomass of acidic tundra ranged from 150.5 ± 16.60 g/m² at 5 m from the road to 743.1 ± 168.98 g/m² at 100 m from the road. Species richness in acidic tundra next to the road was less than half of that at 100 m away from the road. Community composition was altered most noticeably in acidic tundra. The moss *Tomentypnum nitens*, dominant in nonacidic arctic tussock tundra, was nearly equally abundant at all distances from the road at the nonacidic tundra site, whereas *Sphagnum* mosses, dominant in acidic low arctic tussock tundra, were virtually eliminated near the road at the acidic tundra site. *Salix lanata* was more abundant next to the road at the nonacidic site. Ordinations indicate that variation in vegetation cover is explained by distance from the road. Knowledge of differential effects of road construction and use, including the long-term effects of hydrological alterations and dust mobilization on local corridors, is key information for planning development in areas of arctic tundra. Planned placement of roads in the future should consider the impact of such changes to sensitive (acidic) tundra areas in the Arctic.

Key words: Alaska; arctic tundra; biomass; disturbance; dust; ordination; permafrost; Sphagnum; Trans-Alaska Pipeline; tundra vegetation.

INTRODUCTION

The presence of continuous permafrost (perennially frozen ground) complicates planning, construction, and use of paved roads. Seasonal freezing and thawing of the ground surface result in heaving and shifting of surface materials and can result in subsequent breakage of pavement (Berg 1980). Gravel roads, which can be more easily maintained, are therefore widely used in permafrost areas to minimize the incidence of such road damage. Heavy travel on these roads, however, introduces severe, chronic dust deposition in surrounding ecosystems. Other road-related impacts include blockage of natural drainage patterns, alteration of snow drift patterns, off-road vehicle trails, gravel spray, and toxic spills (Walker et al. 1987, Walker 1996). The Dalton Highway is a gravel road that parallels the Trans-Alas-

ka Pipeline on the North Slope of Alaska, from just north of Fairbanks to Prudhoe Bay on the northern coast. We contrasted effects of disturbance from the Dalton Highway on nonacidic and acidic tundra.

Our primary goal was to contrast road-related changes in substrate properties, biomass, and species composition at two tundra sites that had initially different substrate pH and species composition. We hypothesized that because road materials in this region are primarily of calcareous alluvial origin, initial substrate pH would control the degree of response to road dust disturbance. Although all tundra communities may be affected from the road disturbance, we expected that acidic tundra species composition would be altered more than nonacidic tundra.

Road impacts include both direct effects, such as dust deposition, and indirect effects, such as changes to surface albedo. Chronic disturbance in some areas along the Dalton Highway and roads associated with the coastal oil fields has resulted in cumulative impacts

that have affected the tundra ecosystem beyond what was predicted at the time of the initial road construction. Walker and Everett (1987) provided an overview of dust impacts on arctic tundra. They noted that the impacts to acidic and nonacidic tundra were quite different, but provided little quantitative data. Short-term responses of vegetation to artificially increased substrate pH may be subtle (Mackun et al. 1994), but acidophilic vegetation is adversely affected over the long term (Brown 1988). Based on these earlier studies, the substrate changes we expected to see near the road included increased soil pH, increased nutrient availability, a shallower organic horizon, higher bulk density, lower soil moisture, altered snowpack, and deeper active-layer thaw in sites near the road. We also expected to find decreases in aboveground biomass next to the road, particularly in mosses, lichens, forbs, and evergreen shrubs, along with an increase in graminoid and deciduous shrub biomass. This paper provides a quantitative analysis contrasting changes to substrate and vegetation in acidic and nonacidic tundra after 15 yr of road and dust impact. Whereas both acidic and nonacidic tundra and the dominant species associated with each are common in the Arctic, the disturbance patterns linked to road disturbance that are assessed in this study provide insight into future plans for Arctic development. Consideration of the potential for ecosystem damage in specific areas will help minimize negative consequences.

METHODS

Study area

The Dalton Highway is a gravel road that was built to access the region of northern Alaska between Fairbanks and the Prudhoe Bay oil fields (Fig. 1) and to aid in construction and maintenance of the Trans-Alaska Pipeline. The northern section of the Dalton Highway, where the study area is located, was built in 1974. The road traverses the continuous permafrost zone (Brown and Berg 1980), where seasonal thaw (active-layer thickness) is generally <0.5 m (Brown 1980). The road is composed of a raised gravel bed up to 1.5 m in thickness, so as to minimize seasonal thaw penetration (Berg 1980). Gravel roadbed materials were quarried from bedrock outcrops or from calcareous alluvial deposits (Walker and Everett 1991).

Two study sites adjacent to the gravel Dalton Highway were selected on the basis of substrate pH, homogeneity of vegetation cover type, and history of previous research (Everett 1980a, b, Walker and Werbe 1980, Werbe 1980). Although time and intensity of the research restricted this study to just the two sites, the two areas selected were typical of vegetation types occurring on broad uplands of the Foothills and many parts of the Coastal Plain on the North Slope of Alaska. Subsequent comparisons of our data with earlier studies (Walker and Everett 1987) give qualitative confirma-

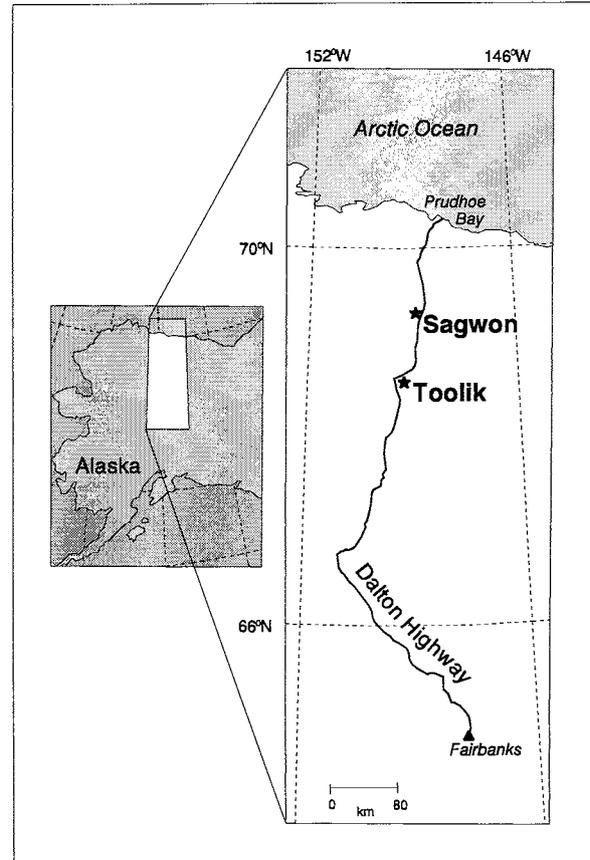


FIG. 1. Location of the study area in northern Alaska. Study sites Sagwon (nonacidic tundra) and Toolik (acidic tundra) are located adjacent to the Dalton Highway, a gravel road built to access the region between Fairbanks and Prudhoe Bay, where oil fields are located. The section of the road where the study area is located was built in 1974.

tion that road and dust are affecting the ecosystem all along the Dalton Highway in a similar manner. Both study sites were situated on relatively extensive (>500 m) of homogeneous vegetation on both sides of the road, level, upland areas. The terms acid and nonacid, as used here, are roughly equivalent to their usage in the U.S. Soil Taxonomy (Anonymous 1975). Sites with soil pH < 5.0 are considered acidic, and sites with soil pH ≥ 5.0 are considered nonacidic.

The Sagwon site ($69^{\circ}27' N$, $148^{\circ}38' W$; 251 m above sea level) is on a nonacidic substrate, located in the northern section of the Arctic Foothills in an area influenced by input of wind-blown calcareous loess from the Sagavanirktok River (Lawson 1980). The continued deposition of calcareous loess contributes toward maintaining an alkaline to circumneutral substrate (Walker and Everett 1991). Soil is generally loamy, has a nonacid peaty surface layer, and is poorly drained with a shallow permafrost table (Everett 1980b). The original vegetation at Sagwon was a relatively homogeneous cover of moist, sedge, dwarf-shrub tundra dominated by *Carex bigelowii*, *Dryas integrifolia*, *Salix reticulata*,

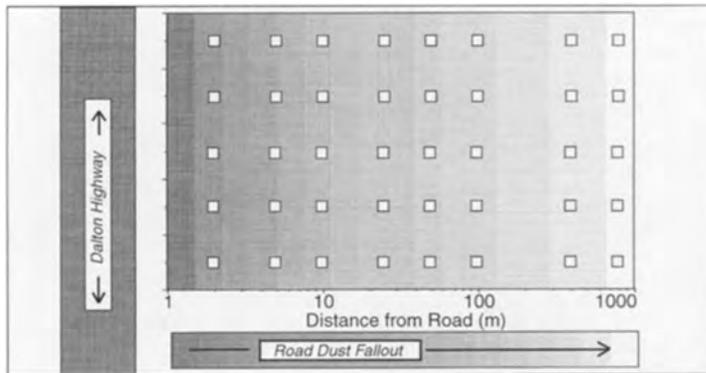


FIG. 2. Generalized diagram of sampling scheme at both sites. Study was designed to account for logarithmically distributed fallout of road dust (Everett 1980a). Replicate sample plots (represented as squares) were placed 20 m apart along eight 100-m parallel transects spaced at (approximately) logarithmically scaled distances from the road.

Tomentypnum nitens, and scattered low shrubs of *Salix lanata* ssp. *richardsonii*. This vegetation type is dominant on relatively stable, well-drained, alkaline or near-neutral sites in the Arctic Foothills (Walker et al. 1994).

The Toolik site (68°41' N, 149°10' W; 808 m above sea level) is on an acidic substrate, located in the southern section of the Arctic Foothills in an area of glacial moraine and drift that has been modified by peat development. Soil is loamy, with an acid, peaty surface layer, and poorly drained with a shallow permafrost table (Walker et al. 1989). The nondisturbed vegetation at Toolik was a uniform, moist, tussock-sedge, dwarf-shrub tundra dominated by *Eriophorum vaginatum*, *Betula nana*, *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea*, and *Sphagnum* spp. (Werbe 1980). This vegetation type is characteristically found on stable, acidic sites in the Arctic Foothills (Walker et al. 1994).

Both areas receive significant amounts of road dust, although the Sagwon site receives a slightly higher dust load than the Toolik site (Everett 1980a). Dust composition is similar at both sites, but Ca^+ and Na^+ concentrations are lower in dust at Sagwon and road materials are more alkaline at Toolik (pH 8.3) than at Sagwon (pH 7.6) (Auerbach 1992).

Sample design

Dust loads decrease logarithmically with distance from the road (Everett 1980a), and sample locations were chosen accordingly (Fig. 2). Eight, 100-m transects were established parallel to the road at each site; at 2, 5, 10, 25, 50, 100, 300, and 525 m from the road at Sagwon, and at 2, 5, 10, 25, 50, 100, 400, and 800 m from the road at Toolik. The zone of maximum dust-fall is within the first 300 m from the road (Everett 1980a), and the area beyond this distance is essentially undisturbed. Five replicate plots were sampled in each of the eight transects for a total of 40 samples at each site (replicates were spaced 20 m apart from each other along each transect and parallel to the road). Simple regression was used to test for patterns in substrate properties, biomass amounts, and species composition as they related to log of distance from the road.

Sampling of substrate properties

Soils were sampled from mossy areas between tussocks in July and August of 1989 and 1990. Depth of the organic soil horizon was measured to the nearest centimeter. Soil samples of 250 cm³ were obtained from the base of the fibric (Oi) horizon (the least decomposed layer of the organic soil horizon) at both sites, and an additional sample was taken from the soil surface at Toolik. Wet soils were weighed, then dried in a 105°C oven for at least 24 h. Soil moisture was determined gravimetrically, and bulk density (in grams per cubic centimeter) was calculated as mass of oven-dried soil per sample volume. The soils were analyzed for pH (paste method) and $\text{NO}_3\text{-N}$ and P (in micrograms per gram) ($\text{NH}_4\text{HCO}_3\text{-DTPA}$ method) (Page et al. 1982). Maximum seasonal active-layer thickness (depth from surface to top of the permafrost table) was measured to the nearest centimeter at 10 random points around the 40 sample plots at each site on 29–30 August; disturbed areas were avoided. An average thickness was determined for each plot. Spring snow depth was measured to the nearest centimeter at every 5 m along each transect at both sites on 9–10 May 1991 for a total of 21 sampling points per transect. At this time snowmelt had already progressed considerably at the Toolik site, whereas the melt at the Sagwon site had not yet begun.

Sampling of vegetation characteristics

Vegetation biomass was measured by clip harvest in early August 1989 at Toolik and in late July 1990 at Sagwon. A 20 × 50 cm Daubenmire frame was used to define clipping area. Vegetation was clipped to the top of the organic soil horizon (as indicated by a darker moss color, which implied decomposition rather than photosynthesis was taking place). Vegetation was sorted into live, dead, and woody fractions of evergreen shrubs, deciduous shrubs, forbs, graminoids, horsetails, mosses, and lichens. Vegetation fractions were oven-dried at 100°C for 24 h and weighed.

The point-quadrat method (Mueller-Dombois and Ellenberg 1974) was used for estimating plant cover. Sampling was conducted in early August 1989 at Toolik and in late July 1990 at Sagwon. The aluminum point-

TABLE 1. Statistical results from regressions of variables on log of distance from the road at the two study sites (regression model: test variable = $a + b$ (log of distance from the road)).

| Test variables | Sagwon | | | | Toolik | | | |
|--|----------|----------|-----------------------|----------|----------|----------|-----------------------|----------|
| | <i>a</i> | <i>b</i> | <i>r</i> ² | <i>P</i> | <i>a</i> | <i>b</i> | <i>r</i> ² | <i>P</i> |
| Substrate property | | | | | | | | |
| pH (soil surface) | ... | ... | ... | ... | 7.98 | -1.51 | 0.90 | <0.0001 |
| pH (fibric layer) | 7.07 | -0.26 | 0.32 | <0.0001 | 5.48 | -0.60 | 0.49 | <0.0001 |
| Soil NO ₃ -N (soil surface) | ... | ... | ... | ... | -3.42 | 23.04 | 0.76 | <0.0001 |
| Soil NO ₃ -N (fibric layer) | 1.3 | 10.78 | 0.67 | <0.0001 | 14.08 | 16.04 | 0.49 | <0.0001 |
| Soil P (soil surface) | ... | ... | ... | ... | -12.25 | 62.85 | 0.60 | <0.0001 |
| Soil P (fibric layer) | -21.03 | 63.99 | 0.81 | <0.0001 | 20.30 | 19.84 | 0.31 | 0.0002 |
| Organic horizon depth | 29.52 | -3.64 | 0.21 | 0.0030 | 18.86 | 3.90 | 0.34 | <0.0001 |
| Bulk density | 0.35 | -0.14 | 0.67 | <0.0001 | 0.28 | -0.10 | 0.68 | <0.0001 |
| Soil moisture | 74.20 | 157.56 | 0.72 | <0.0001 | -29.17 | 218.22 | 0.72 | <0.0001 |
| Active-layer thaw depth | 65.98 | -11.17 | 0.57 | <0.0001 | 55.50 | -6.77 | 0.73 | <0.0001 |
| Spring snow depth | 74.71 | -21.84 | 0.62 | <0.0001 | -2.70 | 4.34 | 0.21 | <0.0001 |
| Aboveground biomass | | | | | | | | |
| Total live aboveground | 310.05 | 114.24 | 0.29 | 0.0003 | 79.16 | 239.60 | 0.48 | <0.0001 |
| Lichens | -10.48 | 14.75 | 0.28 | 0.0004 | -2.05 | 19.09 | 0.08 | 0.0705 |
| Mosses | 106.76 | 152.13 | 0.41 | <0.0001 | -80.67 | 231.72 | 0.51 | <0.0001 |
| Forbs | 1.96 | 0.76 | 0.05 | 0.1769 | -0.72 | 0.75 | 0.21 | 0.0028 |
| Graminoids | 104.21 | -35.30 | 0.31 | 0.0002 | 137.75 | -47.80 | 0.44 | <0.0001 |
| Deciduous shrubs | 18.10 | -4.78 | 0.10 | 0.0530 | 2.43 | 1.39 | 0.06 | 0.1410 |
| Evergreen shrubs | 28.93 | -0.91 | 0.00 | 0.7986 | 19.83 | 9.66 | 0.13 | 0.0236 |
| Species richness | | | | | | | | |
| Total recorded species | 12.17 | 1.40 | 0.13 | 0.0234 | 10.87 | 4.10 | 0.49 | <0.0001 |

Note: ... = no data.

quadrat frame was 1 m² in size, with double-layer strings spaced 10 cm apart to make a 10 × 10 grid for a total of 100 sample points per plot. Species were recorded at the top and bottom of the canopy at each point. Plants were identified using Hultén (1968) for most of the vascular species, Argus (1973) for the *Salix*, Hale (1969) and Thomson (1984) for the lichens, and Conard (1956) and Vitt et al. (1988) for some of the mosses. Field identification of *Sphagnum* specimens was according to Andrus (1980), Lange (1982), and Nyholm (1969); mosses unidentified in the field were identified in the laboratory by Dr. Dale Vitt, University of Alberta. Species cover values were regressed against distance to the road. Because vascular plants characteristically constitute the top layer of the vegetation canopy, top canopy frequencies of vascular species were used in regressions, and bottom canopy frequencies of liverworts, mosses, and lichens were used.

Species richness was estimated as the total number of different species recorded in either the top or bottom of the vegetation canopy. Total species richness is not measured with the point quadrat, but the method does provide an estimate of overall community richness, even though less abundant species may not be included in the measure.

Ordination of vegetation samples was performed using detrended correspondence analysis (DCA) (Hill and Gauch 1980) with the program CANOCO (ter Braak 1987). Ordinations were based on species frequencies in the top layer of the plant canopy. Three ordinations were produced: one for each of the two individual sites, and one for a combination of both sites. Rare species

were downweighted within CANOCO to emphasize importance of dominant species. Environmental variables were related to the ordination axes by determining Pearson product-moment correlation coefficients between the unconstrained ordination axes and environmental variables, indicating the degree of linear relationship. Biplot scores of environmental variables calculated by CANOCO were used to produce sample-environment biplots. In these plots, the environmental variables are represented by arrows, where the arrow points in the direction of maximum change in value of the variable (ter Braak 1987). Environmental variables used in the analysis include fibric horizon soil moisture, bulk density, pH, percent organic matter, NO₃-N, and P.

RESULTS

Substrate properties

The regressions of all measured substrate properties with distance from the road were significant at both sites (Table 1). Soil pH was higher close to the road at both sites, although the gradient was steeper at Toolik (Fig. 3, Table 1). At Toolik, 90% of the variation in surface soil pH was explained by distance from the road. At 2 m from the road, surface soil pH was 7.3 ± 0.07 (mean \pm 1 SE), and a pH of 4.0 ± 0.05 was measured at 800 m. In the fibric layer, the pH was 5.5 ± 0.48 at 2 m from the road and 4.1 ± 0.06 at 800 m from the road, with 49% of the variance explained by road distance. At Sagwon, mean pH in the fibric soil horizon was 7.1 ± 0.07 at 2 m from the road, and 6.7 ± 0.12 at 525 m. Road-explained variation in soil pH

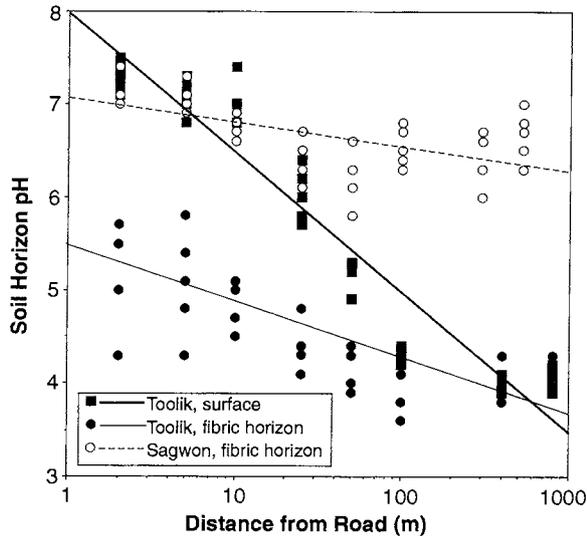


FIG. 3. Soil horizon pH at the Sagwon and Toolik study sites. Soil pH decreases to a normal level with increasing distance from the road at both sites. Each symbol represents a sample value for each plot at a site; symbol overlap may occur where plots have equal values. Samples were regressed against log of distance from the road; see Table 1 for regression line equations and significance of relationships.

was 32% at Sagwon. Plant-available $\text{NO}_3\text{-N}$ was statistically lower near the road at Toolik, and the gradient with distance from the road was steeper than at Sagwon, although $\text{NO}_3\text{-N}$ was also statistically lower near the road at Sagwon (Fig. 4, Table 1). Steep gradients in plant-available P were measured at the soil surface at Toolik and in the fibric horizon at Sagwon; fibric horizon P was not as strongly affected at Toolik (Fig. 4, Table 1). At Toolik, the organic soil horizon was generally shallower near the road as expected, whereas at Sagwon, the opposite trend occurred (Fig. 4, Table 1). Soils in close proximity to the road had higher bulk density than soils farther from the road at both sites (Fig. 4, Table 1). At both sites, gravimetric soil moisture was lower near the road, although the gradient was steeper at Toolik (Fig. 4, Table 1). This trend was most likely due to the higher bulk density of soils near the road.

Maximum depth of active-layer thaw was deepest next to the road at both sites (Fig. 4, Table 1). At Sagwon, the depth of thaw at 2 and 5 m from the road averaged 71 ± 1.3 and 64 ± 1.3 cm, respectively, as compared to 41 ± 0.9 cm at 525 m. Distance from the road accounted for 57% of the variance at Sagwon. At Toolik, maximum thaw next to the road at 2 m was 54 ± 0.7 cm, and depth decreased consistently with increased distance from the road to 38 ± 0.9 cm at 800 m from the road. Road distance explained 73% of the variance in thaw depth at Toolik.

The spring 1989 snowpack was deep next to the road at Sagwon, whereas snowpack was shallow next to the road at Toolik (Fig. 4, Table 1). Overall, mean snow

depth at Sagwon ranged from 21 ± 2.0 cm at 300 m from the road to 71 ± 2.8 cm at 5 m from the road. At Sagwon there was a drift extending out to 10 m from the road (as measured by snow depth in the 2-, 5-, and 10-m transects) which was noticeably deeper than the normal snowpack occurring away from the road. Overall snow depth at Toolik ranged from 0 ± 0.4 cm at 10 m from the road to 19 ± 2.6 cm at 400 m. Most of the snow next to the road at Toolik had melted by the measurement day of 9 May, and only small patches of snow remained.

Vegetation characteristics

Biomass.—Total biomass (mosses, lichens, and live vascular plants) was lower next to the road, compared to distances farther from the road, at both sites. More variation was explained by distance from the road at Toolik (48 vs. 29%) and the gradient was steeper (Fig. 5, Table 1). At Toolik, the lowest biomass measured was 150.5 ± 16.60 g/m^2 at 5 m and the greatest was 743.1 ± 168.98 g/m^2 at 100 m. At Sagwon, biomass varied between 330.0 ± 34.72 g/m^2 at 2 m and 690.7 ± 94.52 g/m^2 at 100 m. Lichen and moss biomass were lower next to the road at Sagwon; forb and evergreen shrub biomass were not statistically related to distance from the road at Sagwon. At Toolik, biomass of mosses, forbs, and evergreen shrubs decreased with proximity to the road. Lichen biomass at Toolik ranged from 0.0 ± 0.02 g/m^2 next to the road to 86.1 ± 56.97 g/m^2 in a middle transect, but variation was not statistically explained by a road effect. Graminoids were the only growth form to have significantly higher biomass closer to the road at both sites; in some plots, graminoid biomass next to the road was twice that of undisturbed plots. Deciduous shrubs also showed a trend of increased biomass next to the road at Sagwon, but not at Toolik.

Species richness.—Species richness varied minimally with distance from the road at Sagwon, whereas at Toolik there was more of a road effect (Fig. 6, Table 1). Only 13% of the variation in species richness was explained by a road effect at Sagwon, as compared to 49% at Toolik. Total species richness recorded in the top canopy at Sagwon ranged from 13 ± 1.0 species at 2 m to 17 ± 1.1 species at 50 m. At Toolik, the range was between 9 ± 1.3 species at 2 m and 22 ± 1.9 species at 800 m.

Species cover.—Vegetation cover was less variable with distance from the road at Sagwon compared to Toolik. In particular, cover of the dominant moss in nonacidic tundra, *Tomentypnum nitens*, was fairly uniform at all distances from the road, and was not related to distance from the road at Sagwon ($r^2 = 0.04$; $P = 0.2074$) (Fig. 7). In contrast, cover of the dominant moss in acidic tundra, *Sphagnum* spp., was highly correlated with road distance at Toolik ($r^2 = 0.662$; $P < 0.0001$).

Overall, species cover patterns relative to distance

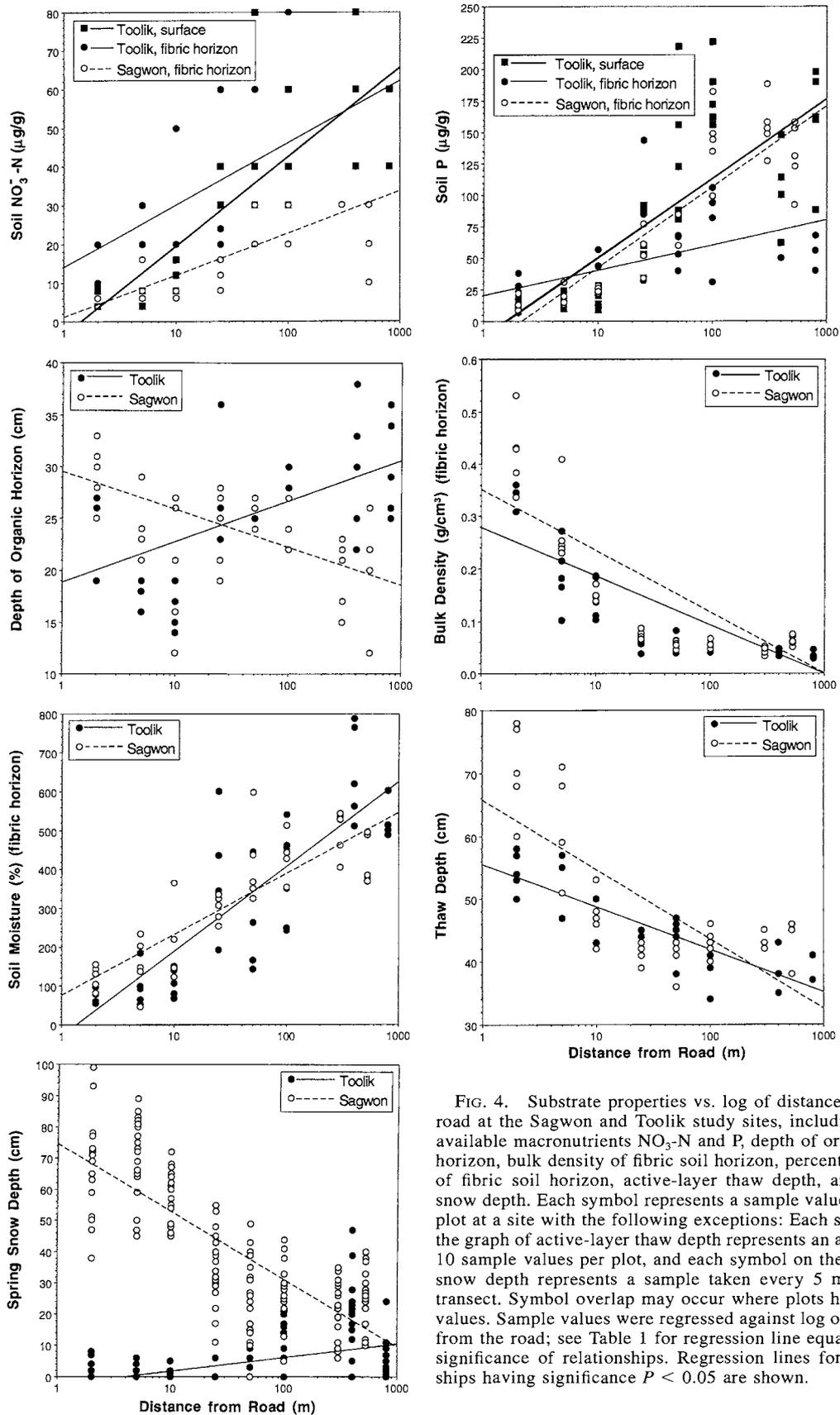


FIG. 4. Substrate properties vs. log of distance from the road at the Sagwon and Toolik study sites, including plant-available macronutrients $\text{NO}_3^- \text{N}$ and P, depth of organic soil horizon, bulk density of fibric soil horizon, percent moisture of fibric soil horizon, active-layer thaw depth, and spring snow depth. Each symbol represents a sample value for each plot at a site with the following exceptions: Each symbol on the graph of active-layer thaw depth represents an average of 10 sample values per plot, and each symbol on the graph of snow depth represents a sample taken every 5 m along a transect. Symbol overlap may occur where plots have equal values. Sample values were regressed against log of distance from the road; see Table 1 for regression line equations and significance of relationships. Regression lines for relationships having significance $P < 0.05$ are shown.

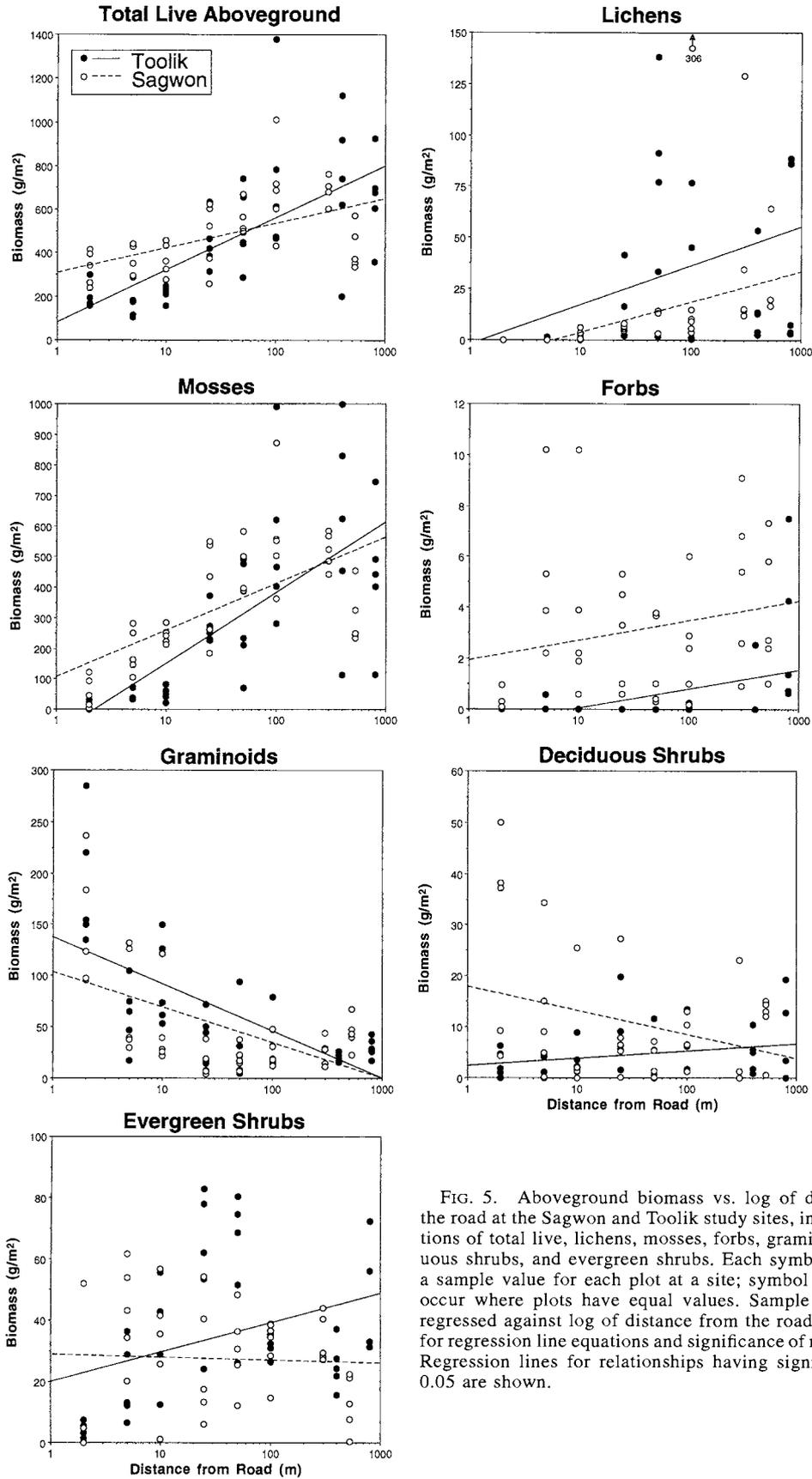


FIG. 5. Aboveground biomass vs. log of distance from the road at the Sagwon and Toolik study sites, including fractions of total live, lichens, mosses, forbs, graminoids, deciduous shrubs, and evergreen shrubs. Each symbol represents a sample value for each plot at a site; symbol overlap may occur where plots have equal values. Sample values were regressed against log of distance from the road; see Table 1 for regression line equations and significance of relationships. Regression lines for relationships having significance $P < 0.05$ are shown.

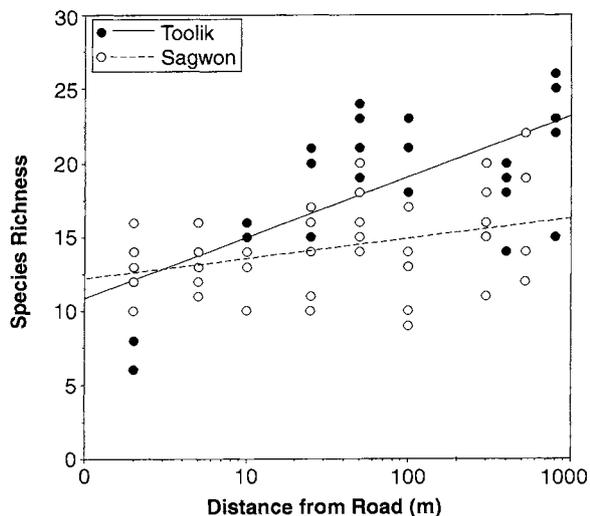


FIG. 6. Species richness vs. log of distance from the road at the Sagwon and Toolik study sites. Richness was determined by total number of species measured in a plot using the point quadrat method. Each symbol represents a sample value for each plot at a site; symbol overlap may occur where plots have equal values. Sample values were regressed against log of distance from the road; see Table 1 for regression line equations and significance of relationships.

from the road were similar to biomass patterns (Table 2). At Sagwon, graminoids *Eriophorum angustifolium* and *E. vaginatum* had significantly higher cover near the road. Cover of the willow *Salix lanata* ssp. *richardsonii* was particularly high in the transect 2 m from the road ($13.2 \pm 6.61\%$ at 2 m, $0.0 \pm 0.00\%$ at 525 m). Cover of the lichens *Peltigera aphthosa*, *Cetraria cucullata*, *C. islandica*, *Thamnolia subuliformis*, and bryophytes *Aulacomnium acuminatum*, *A. turgidum*, *Dicranum groenlandicum*, *Hylocomium splendens*, and *Ptilidium ciliare*, was significantly lower near the road. *Limprichtia revolvens* (= *Drepanocladus revolvens*) was the only moss with significantly higher cover near the road at Sagwon.

At Toolik, cover of graminoids *Eriophorum vaginatum* and *Festuca rubra* and the deciduous shrub *Rubus chamaemorus* was significantly higher near the road. The forb *Pedicularis lapponica*, the evergreen shrubs *Ledum palustre* ssp. *decumbens*, and *Vaccinium vitis-idaea* ssp. *minus*, lichens *Cetraria cucullata*, *Cladonia amaurocraea*, *Cladonia rangiferina*, *Dactylina arctica*, and *Peltigera canina*, *Sphagnum* mosses *Sphagnum lenense*, *S. balticum*, and *S. rubellum*, and bryophytes *Anastrophyllum minutum*, *Dicranum angustum*, *D. spadicum*, and *Lophozia binsteadii* all had significantly lower cover near the road. The mosses *Bryum pseudotriquetrum*, *Distichium inclinatum*, and *Tortula ruralis* had significantly higher cover near the road.

There were also extensive, distinct, bands of dominant mosses distributed relative to the road at Toolik. Cover of mosses was significantly different (at least P

< 0.01) in these transects as compared with other transects. The moss bands appear to be associated with different levels of dust disturbance (Fig. 8). Next to the road (in transects at 2, 5, and 10 m from the road), there was high cover of weedy mosses (including *Bryum* spp., *Ceratodon purpureus*, and *Tortula ruralis*) on the mineral substrate created by very high dust loads. *Aulacomnium turgidum* was more abundant at 25 m than in other transects. *Dicranum* spp. were higher in cover at 25, 50, and 100 m from the road, and cover of *Sphagnum* spp. was high at 100, 400, and 800 m. The moss *Polytrichum juniperinum* had relatively high cover at 800 m.

Vegetation–environment relationships.—The first axis of the Sagwon ordination had an eigenvalue of 0.30, and the axis is strongly correlated ($P < 0.01$) with the log of distance from the road (Fig. 9, Table 3). All of the environmental variables are also highly correlated ($P < 0.01$) with the first axis. However, these correlations appear to be most strongly controlled by the samples at 2 m, which had a higher abundance of sedges and deciduous shrubs and a lower abundance of bryophytes and forbs in comparison with the rest of the samples, and cluster at the left side of the ordination diagram. The samples at increasing distances from the road become intermingled on the diagram.

The second axis had an eigenvalue of only 0.16. No road-related patterns are discernible in the second axis, and pH is the only environmental variable that is significantly correlated. Minimal grouping on the ordi-

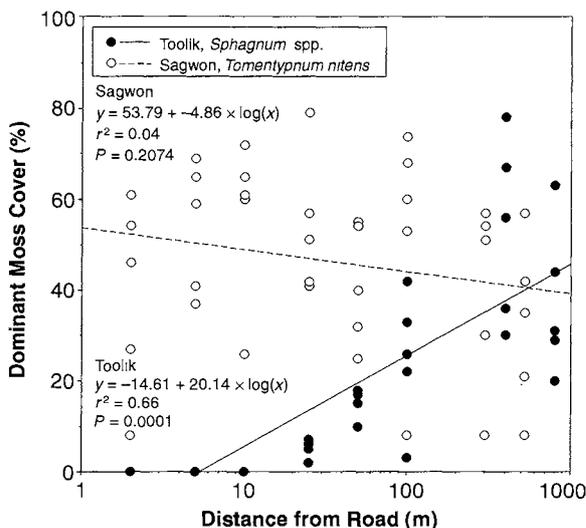


FIG. 7. Cover of dominant mosses vs. log of distance from the road at the Sagwon and Toolik study sites. Cover of *Tomentypnum nitens*, the dominant moss at Sagwon, appears to be homogeneous and unrelated to distance from the road. Cover of *Sphagnum* spp., the dominant moss at Toolik, appears to be highly dependent on distance from the road. Each symbol represents a sample value for each plot at a site; symbol overlap may occur where plots have equal values. Sample values were regressed against log of distance from the road.

TABLE 2. Significant ($P < 0.05$) results of regressing species cover on log of distance from the road at the two study sites (regression model: species cover = $a + b$ (log of distance from the road)).

| Species | a | b | r^2 | P |
|---|--------|---------|-------|--------|
| Sagwon | | | | |
| Liverworts | | | | |
| <i>Ptilidium ciliare</i> | -0.798 | 1.267 | 0.18 | 0.0060 |
| Lichens | | | | |
| <i>Peltigera aphthosa</i> | -0.655 | 0.963 | 0.29 | 0.0003 |
| <i>Cetraria cucullata</i> | -0.300 | 0.472 | 0.19 | 0.0050 |
| <i>Cetraria islandica</i> | -0.135 | 0.218 | 0.14 | 0.0160 |
| <i>Thamnolia subuliformis</i> | -0.360 | 0.364 | 0.14 | 0.0184 |
| Mosses | | | | |
| <i>Aulacomnium acuminatum</i> | -1.007 | 1.940 | 0.25 | 0.0010 |
| <i>Aulacomnium turgidum</i> | -0.658 | 1.339 | 0.15 | 0.0140 |
| <i>Dicranum groenlandicum</i> | -0.595 | 0.843 | 0.19 | 0.0049 |
| <i>Hylocomium splendens</i> | 2.690 | 7.425 | 0.30 | 0.0003 |
| <i>Limprichtia revolvens</i> (= <i>Drepanocladus revolvens</i>) | 6.154 | -2.313 | 0.17 | 0.0084 |
| Graminoids | | | | |
| <i>Eriophorum angustifolium</i> | 3.001 | -1.465 | 0.19 | 0.0054 |
| <i>Eriophorum vaginatum</i> | 32.119 | -8.293 | 0.17 | 0.0084 |
| Deciduous shrubs | | | | |
| <i>Salix lanata</i> ssp. <i>richardsonii</i> | 7.673 | -3.643 | 0.20 | 0.0039 |
| Toolik | | | | |
| Liverworts | | | | |
| <i>Anastrophyllum minutum</i> | -0.404 | 0.463 | 0.14 | 0.0156 |
| <i>Barbilophozia binsteadii</i> | -0.251 | 0.270 | 0.12 | 0.0297 |
| Lichens | | | | |
| <i>Cetraria cucullata</i> | -0.161 | 2.419 | 0.34 | <.0001 |
| <i>Cladonia amaurocraea</i> | -0.446 | 1.283 | 0.22 | 0.0024 |
| <i>Cladonia rangiferina</i> | -0.268 | 0.853 | 0.14 | 0.0186 |
| <i>Dactylina arctica</i> | -0.480 | 0.717 | 0.42 | <.0001 |
| <i>Peltigera canina</i> | -0.095 | 0.092 | 0.13 | 0.0230 |
| Mosses | | | | |
| <i>Bryum pseudotriquetrum</i> | 8.477 | -3.794 | 0.23 | 0.0020 |
| <i>Dicranum angustum</i> | 0.836 | 2.056 | 0.11 | 0.0373 |
| <i>Dicranum spadiceum</i> | -0.201 | 1.255 | 0.12 | 0.0256 |
| <i>Distichium inclinatum</i> | 4.507 | -1.766 | 0.23 | 0.0019 |
| <i>Sphagnum lenense</i> | -7.667 | 8.613 | 0.51 | <.0001 |
| <i>Sphagnum balticum</i> | -6.838 | 9.165 | 0.48 | <.0001 |
| <i>Sphagnum rubellum</i> | 0.191 | 1.132 | 0.16 | 0.0102 |
| <i>Tortula ruralis</i> | 8.414 | -3.294 | 0.23 | 0.0018 |
| Forbs | | | | |
| <i>Pedicularis lapponica</i> | -0.201 | 0.239 | 0.17 | 0.0086 |
| Graminoids | | | | |
| <i>Eriophorum vaginatum</i> | 62.943 | -13.550 | 0.45 | <.0001 |
| <i>Festuca rubra</i> | 0.189 | -0.088 | 0.12 | 0.0296 |
| Deciduous shrubs | | | | |
| <i>Rubus chamaemorus</i> | 3.373 | -0.872 | 0.15 | 0.0135 |
| Evergreen shrubs | | | | |
| <i>Ledum palustre</i> ssp. <i>decumbens</i> | 4.257 | 1.995 | 0.14 | 0.0159 |
| <i>Vaccinium vitis-idaea</i> ssp. <i>minus</i> | 2.751 | 1.681 | 0.16 | 0.0114 |

nation diagram of samples taken at the same distance from the road suggests that there is at least as much variation in vegetation composition of samples within transects as there is variation between transects.

The first axis of the Toolik ordination had an eigenvalue of 0.26 and was also highly correlated ($P < 0.01$) with distance from the road (Fig. 9, Table 4). All of

the environmental variables are strongly correlated ($P < 0.01$) with the first axis. The Toolik ordination differed from the Sagwon ordination by more closely grouping the samples according to distance from road, suggesting that road effects controlled vegetation patterns to a greater distance at Toolik. Groups of sample points are spaced along the first axis from left to right

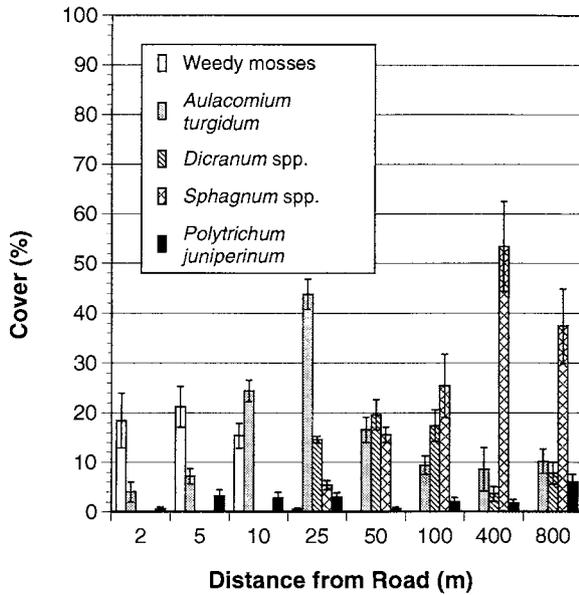


FIG. 8. Cover (five-plot mean \pm 1 SE) of selected mosses at the Toolik study site, illustrating peaks in abundance of mosses with distance from the road in acidic tundra that are significantly different ($P < 0.01$) from their cover in other transects. This phenomenon appears to correspond to individual ability to compete and respond to road and dust disturbance. Weedy mosses *Bryum* spp., *Ceratodon purpureus*, and *Tortula ruralis* were particularly abundant at 2, 5, and 10 m from the road. *Aulacomium turgidum* peaked in abundance at 25 m, *Dicranum* spp. were unusually high in cover at 25, 50, and 100 m, *Sphagnum* spp. were high in cover at 400 and 800 m, and *Polytrichum juniperinum* was relatively abundant at 800 m from the road.

across the diagram, according to distance from the road (with the exception of the 400- and 800-m samples, which were predicted as being beyond the extent of major dust effects).

The second axis of the Toolik ordination also appears to separate samples according to distance from the road, although it had an eigenvalue of only 0.10. This axis primarily indicates a spread of samples occurring at far distances (400 and 800 m) from the road. Samples

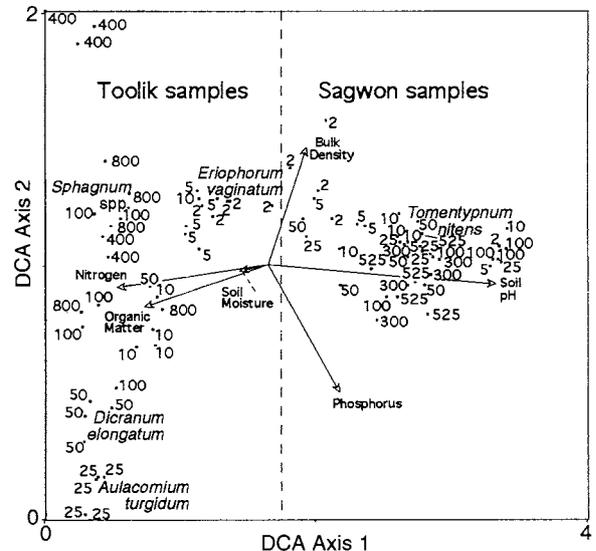
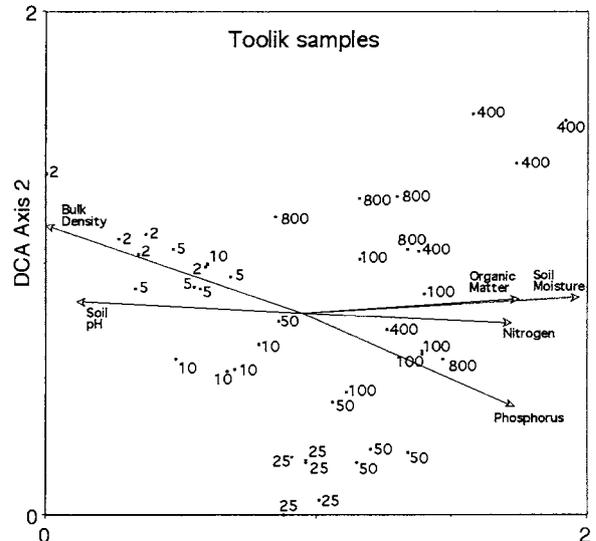
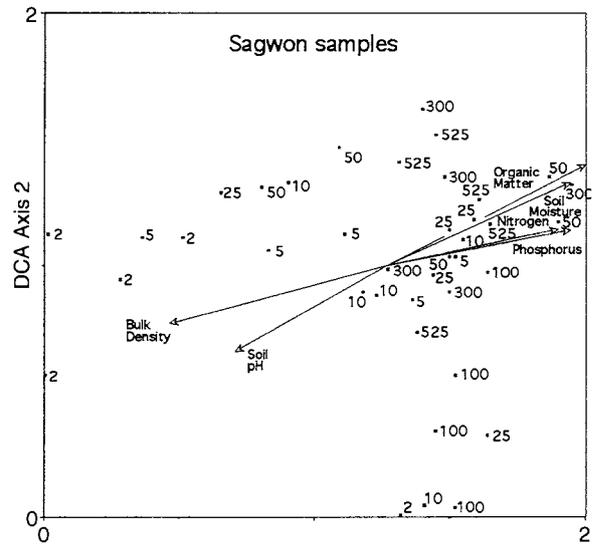


FIG. 9. Detrended correspondence analysis (DCA) ordination of samples by species cover at the Sagwon study site, the Toolik study site, and both the Sagwon and Toolik study sites. Numbers on the graphs indicate sample transect distance from the road. Arrows on the graphs are derived from correlation coefficients between each of the quantitative environmental variables and each of the ordination axes; they point in the direction of maximum variation in value of each of the environmental variables. The direction that the arrow is pointing indicates correlation of samples with the environmental variable: arrows pointing toward samples indicate positive correlations, perpendicular arrows indicate lack of correlation, and arrows pointing in the opposite direction indicate negative correlation (Jongman et al. 1987). Coordinates for the origin of the arrows are equal to the mean of the sample axes.

TABLE 3. Correlation matrix of DCA axes and environmental variables for Sagwon site. Values shown are Pearson product-moment correlation coefficients (r).

| | DCA Axis 2 | Soil moisture | Bulk density | Soil pH | Organic matter | NO ₃ -N | P | Log of distance from road |
|--------------------|------------|---------------|--------------|----------|----------------|--------------------|----------|---------------------------|
| DCA Axis 1 | 0.024 | 0.790** | -0.768** | -0.610** | 0.841** | 0.836** | 0.830** | 0.874** |
| DCA Axis 2 | | 0.093 | 0.279 | 0.422** | 0.026 | 0.087 | 0.219 | 0.119 |
| Soil moisture | | | -0.791** | -0.565** | 0.841** | 0.805** | 0.824** | 0.849** |
| Bulk density | | | | 0.726** | -0.815** | -0.711** | -0.705** | -0.821** |
| Soil pH | | | | | -0.649** | -0.540** | -0.503** | -0.567** |
| Organic matter | | | | | | 0.801** | 0.856** | 0.929** |
| NO ₃ -N | | | | | | | 0.802** | 0.821** |
| P | | | | | | | | 0.898** |

* $P < 0.05$, ** $P < 0.01$; $df = 38$.

in the transects farther from the road had more species richness than samples in transects closer to the road. It may be that their placement on the diagram is more influenced by different, rarer species, resulting in more scattering of their sample points. Samples from transects that tended to be dominated by one species appear to be more tightly clustered. None of the environmental variables are significantly correlated with the second axis.

The sites were also ordinated together to examine overall patterns in species composition of samples within and between sites (Fig. 9). The first axis separates the two sites, indicating the unique species composition at each site. This axis had an eigenvalue of 0.63. Substrate pH is the environmental variable most highly correlated ($r = 0.597$; $P < 0.01$) with the axis (Table 5), and accounts for the most variation in species presence between Toolik and Sagwon along the first axis. Samples near the road at Toolik appear to be approaching the vegetation composition of the nonacidic site, and ordinate somewhat intermediate between the two; the high abundance of sedges such as *Eriophorum vaginatum* near the road at both sites is likely causing this convergence. There is minimal grouping of Sagwon samples with distance from the road: Samples with high sedge and shrub cover (at 2 and 5 m from the road) ordinated to the left, the rest of the samples with greater abundances of other taxa ordinated to the right. On the Toolik side of the ordination, samples that had virtually no bryophyte cover (at 2 and 5 m from the

road), ordinated to the right; the samples at 10 m from the road and beyond had substantial bryophyte cover and were ordinated to the left.

The second axis of the combined ordination separated Toolik samples according to road distance. This axis had an eigenvalue of 0.19, and none of the environmental variables are very highly correlated with it (Table 5). The axis appears to be expressing the variation in abundance of bryophyte species at certain distances from the road at Toolik. The high abundance of the mosses *Aulacomnium turgidum*, *Dicranum* spp., and *Sphagnum* spp. appears to have influenced the clustering of sample points into road-distance groups. On the Sagwon side of the ordination diagram, only the samples at 2 m from the road were grouped separately. These samples had greater sedge cover and less abundant *Tomentypnum nitens* cover than the other samples.

DISCUSSION

Substrate properties

Most, but not all, substrate gradients were as expected. Next to the road we found higher soil pH, higher bulk density, lower soil moisture, altered snowpack, and deeper active-layer thaw at both sites. Effects on nutrient availability and depth of organic horizon were not exactly as expected. Near the road, soil nutrient availability was lower than expected, and depth of the organic horizon was shallower (as expected) at Toolik, but deeper at Sagwon.

TABLE 4. Correlation matrix of DCA axes and environmental variables for Toolik site. Values shown are Pearson product-moment correlation coefficients (r).

| | DCA Axis 2 | Soil moisture | Bulk density | Soil pH | Organic matter | NO ₃ -N | P | Log of distance from road |
|--------------------|------------|---------------|--------------|----------|----------------|--------------------|----------|---------------------------|
| DCA Axis 1 | 0.024 | 0.793** | -0.817** | -0.884** | 0.887** | 0.845** | 0.705** | 0.862** |
| DCA Axis 2 | | 0.068 | 0.266 | -0.125 | -0.022 | -0.006 | -0.034 | 0.151 |
| Soil moisture | | | -0.734** | -0.823** | 0.840** | 0.831** | 0.699** | 0.848** |
| Bulk density | | | | 0.776** | -0.847** | -0.756** | -0.683** | -0.824** |
| Soil pH | | | | | -0.969** | -0.876** | -0.853** | -0.948** |
| Organic matter | | | | | | 0.899 | 0.848** | 0.949** |
| NO ₃ -N | | | | | | | 0.715** | 0.873** |
| P | | | | | | | | 0.773** |

** $P < 0.01$; $df = 38$.

TABLE 5. Correlation matrix of DCA axes and environmental variables for combination of Sagwon and Toolik sites. Values shown are Pearson product-moment correlation coefficients (r).

| | DCA Axis 2 | Soil moisture | Bulk density | Soil pH | Organic matter | NO ₃ -N | P | Log of distance from road |
|--------------------|------------|---------------|--------------|----------|----------------|--------------------|----------|---------------------------|
| DCA Axis 1 | 0.206 | -0.119 | 0.178 | 0.597** | -0.200 | -0.502** | -0.146 | -0.109 |
| DCA Axis 2 | | -0.051 | 0.294** | 0.020 | -0.165 | -0.132 | -0.163 | -0.051 |
| Soil moisture | | | -0.722** | -0.652** | 0.829** | 0.745** | 0.738** | 0.837** |
| Bulk density | | | | 0.595** | -0.820** | -0.650** | -0.682** | -0.812** |
| Soil pH | | | | | -0.753** | -0.856** | -0.669** | -0.690** |
| Organic matter | | | | | | 0.795** | 0.851** | 0.938** |
| NO ₃ -N | | | | | | | 0.685** | 0.756** |
| P | | | | | | | | 0.825** |

** $P < 0.01$; $df = 78$.

The higher soil pH near the road was caused by calcareous road dust deposition. Mean fibric layer pH near the road at Sagwon (pH 7.1 ± 0.07) has nearly reached the level of the road dust (pH 7.6). At Toolik, substrate pH near the road (fibric layer pH 5.5 ± 0.48 , soil surface pH 7.3 ± 0.07) could potentially still be increased by the road dust contribution (pH 8.3). In addition, at Toolik there is a greater difference between the pH of the dust and unimpacted soils (8.3 vs. 4.0) than at Sagwon (7.6 vs. 6.7).

Soil properties were affected by the road disturbance at both sites. Bulk density was higher next to the road at both sites, due to supplements to the mineral content of the soil next to the road by dust deposition (Everett 1980a), increased decomposition due to warmer soils near the road (Warren Wilson 1957, Douglas and Tedrow 1960), and decreased organic matter accumulation due to species composition changes, particularly a reduction in moss cover. Gravimetric soil moisture was lower next to the road, probably due to the higher bulk density of these soils. Mineral soils have a lower water-holding capacity than organic soils which, due to their porosity and permeability, absorb and retain water (Boelter 1969). The trend of a shallower organic horizon near the road at Toolik was as expected, due to the above-mentioned alterations in bulk density and soil moisture, but the opposite trend occurred at Sagwon and is unexplained.

It was expected that nutrient availability would be higher near the road for several reasons: (1) soil pH has been raised to the optimal range (between 6.0 and 7.7) for nitrification and increased phosphorus availability (Daubenmire 1959); (2) nutrients have been found to be more available to plants in alkaline soils than in acidic soils (Black 1968), because soil pH affects the solubility and availability of various soil minerals (Rorison 1980); (3) acceleration of nutrient cycling and decomposition rates from road-caused increases in soil moisture or active-layer thaw should allow for greater nutrient availability, as these are factors limiting decomposition in cold arctic soils (Chapin et al. 1980); (4) road dust may provide supplemental nutrients to the tundra (Tamm and Troedesson 1955); and (5) dust accumulated on snow over the winter may

contribute a pulse of nitrogen and other soil minerals to the system upon meltout (Warren Wilson 1958). However, N and P were both lower near the road. This is the same pattern observed at Prudhoe Bay along a loess gradient (Walker and Everett 1991). Coarser grained mineral soils near the Sagavanirktok River had lower total available nutrients than fine-grained, more organic rich soils farther from the river, suggesting that the addition of loess has altered the cation-exchange capacity of the soil. A similar situation may occur with the dust-laden soils near roads. Other possible contributing factors may be associated with differing nutrient uptake of vegetation at different distances from the road. Species composition changes near the road may favor plants with greater nutrient uptake efficiency, thereby effectively reducing the nutrient pool (Chapin 1987). Nutrients may be absorbed by vegetation by the end of the growing season, as when the measurements in this study were recorded, and may have been distributed through greater production (Shaver et al. 1986). Graminoid biomass near the road is much higher than away from the road at both sites, and these plants may be altering levels of N and P. Similar processes may be acting in both the nonacidic and acidic tundra, since nutrient levels are lower near the road at both sites.

Maximum seasonal thaw was deeper next to the road at both sites, as predicted. Changes in the depth of the active layer may initiate cryogenic processes such as thermokarst, heaving, and solifluction (Lawson 1986). Depth of seasonal thaw is affected by surface albedo and energy transfer properties (Lachenbruch and Marshall 1969, Jorgenson 1986). Soil properties, vegetation, and snow cover all affect energy transfer to and from the permafrost. Mineral soils, found next to the road, serve to increase the magnitude of heat flux (Brown and Williams 1972). Vegetation cover insulates permafrost from solar energy in the summer, and a decrease in vegetation cover may contribute to deepening of the permafrost thaw (Haag and Bliss 1974). *Sphagnum*, in particular, provides thermal stability to the permafrost (Clymo and Hayward 1982). A deeper than normal snowpack accumulates near the road in the winter, acting as insulation and reducing both penetra-

tion downward of the cold, and also heat loss upward from the soil (Nicholson 1978). Furthermore, the high albedo of white snow decreases the amount of solar radiation penetrating into the soil (Weller and Holmgren 1974). In the spring, however, dust on the snow reduces the albedo (Benson et al. 1975, Holmgren et al. 1975), and a premature spring meltout may occur (Everett 1980a). A deeper seasonal thaw may occur as the active layer begins to thaw earlier and permafrost is exposed to more days of summer insolation.

The contrast of snow depths at the two sites illustrates the manner in which the road affects snow distribution in the two different ways mentioned above. Even though winter snow depths near the road are greater due to drifting in the lee of the raised roadbed, the area next to the road melts earlier in the springtime due to dust-induced changes in albedo. The normal spring snowmelt begins in the foothills of the Brooks Range near the Toolik site and progresses northward towards the Sagwon site (Hinzman et al. 1990). The snowpack measured at Sagwon is illustrative of the winter pattern of snow accumulation in the lee of the road berm, whereas the snowpack measured at Toolik is indicative of the spring pattern of early meltout next to the road. These changes in snow regime potentially affect phenology and plant growth. The onset of vascular plant growth is closely associated with the snowmelt (Tieszen 1974, Webber 1978), as is timing of deciduous shrub and sedge flowering (Larigauderie and Kummerow 1991). Vegetation under snow is protected in the winter from high winds and low temperatures, and receives added moisture (Billings and Bliss 1959), so changed snow conditions may favor some species over others.

Vegetation characteristics

Species composition and vegetation biomass cover were altered next to the road, particularly in the acidic tundra at Toolik. Species most common in anthropogenically disturbed environments are those that under natural conditions grow on disturbance-maintained eroded slopes, landslides, and riverbanks. While many tundra dominants disappear with disturbance, nitrophilous and "pioneering" species of grasses, forbs, and bryophytes become more abundant and community diversity is lowered (Matveyeva 1988). Some changes in species composition may be due to direct effects of the road, such as smothering by dust, whereas other species may be reacting to shifts in nutrient regimes, season length, or a change in the competitive regime caused by the decrease in other key species. The loss of *Sphagnum* mosses may be particularly significant, as these species may act as a "keystone" for controlling ecosystem functions (Jorgenson 1986, Rydin 1986).

Species richness was lower near the road at both sites, more so in the acidic tundra. Plant communities may be simplified by pH-altering disturbance (Brandt and Rhoades 1972). Single-species recovery stages

dominate peat removal areas (Poschlod 1988), and anthropogenically formed tundra communities are floristically poorer than natural communities (Matveyeva 1988). Higher diversity is related to habitat heterogeneity (Alpert and Oechel 1982), and maximal bryophyte species diversity is found in mesic habitats with high microtopographic variation (Vitt and Pakarinen 1977). Lowered species richness, particularly among cryptogams, was found where mechanical disturbance caused reduction of microtopography in tundra (Forbes 1992). At Toolik, *Sphagnum* has died off near the road and single species of bryophytes are now dominant at different distances from the road. *Eriophorum vaginatum* increased next to the road, and the virtually mono-specific sedge community does not provide habitat heterogeneity for bryophytes. More diversity is found in undisturbed acidic tundra where *Sphagnum* modifies the immediate environment, producing more heterogeneous topography (Andrus 1986).

Anthropogenic disturbance to tundra has been found to increase productivity of some plants (Cargill and Chapin 1987). Higher biomass of sedges and shrubs near the road may be attributed to a number of reasons such as: (1) changes in soil environment due to vehicle disturbance as summarized by Chapin and Shaver (1981); (2) increased nutrient availability from dust fallout (Bilgin 1975), (3) a longer growing season (Klinger et al. 1983), and (4) increased water availability from snowmelt (Klinger et al. 1983).

The sedge *Eriophorum vaginatum* gives tussock tundra its characteristic physiognomy, and it is widespread, particularly in acidic areas. *E. vaginatum* has been found to be a particularly successful producer in disturbed conditions (Bliss and Wein 1972, Wein and Bliss 1973, 1974, Chapin and Chapin 1980). Fertilization of undisturbed tundra causes increases in leaf production rate, shoot mass, and tillering in *E. vaginatum* (Shaver and Chapin 1980). Although total soil nutrient availability was lower near the road, it is possible that total nutrient flux is higher (Chapin and Shaver 1981), since nutrient availability was lower near the road. *E. vaginatum* commonly grows under limiting nutrient conditions. Nitrogen appears to be the primary limiting element of *E. vaginatum* growth in Alaska (Shaver et al. 1986), but it also has high nitrogen-use efficiency (low tissue nutrient concentration), allowing it to thrive in low as well as high resource levels (McGraw and Chapin 1989). *E. vaginatum* has a high shoot:root ratio, slow growth (McGraw and Chapin 1989), and effectiveness in translocating nutrients from storage to shoots in spring and subsequently retranslocating them to storage at senescence (Jonasson and Chapin 1985). These are all characteristics of species that appear to be well adapted to disturbance and resource-poor environments (Chapin 1987).

The cover of deciduous shrubs was higher near the road at Sagwon, and evergreen shrubs were less abundant next to the road at both sites. Deciduous shrubs,

such as *Salix* spp., are most likely responding positively to the presence of the deep or protective snowbanks next to the road, which also provides supplemental moisture during the spring melt (Webber et al. 1979, Klinger et al. 1983). *Salix lanata* ssp. *richardsonii*, which grows in nonacidic tundra, seems to be particularly adaptable to the altered conditions near the road. Increased productivity may occur if deciduous shrubs produce larger leaves, thus augmenting photosynthesizing surfaces to make up for leaf area covered by dust (Webber et al. 1979, Werbe 1980). Evergreen plants may experience greater cumulative impact from dust than deciduous plants by retaining leaves from year to year. Dust can clog vascular plant stomata, restricting gas exchange and changing the water balance within the leaf. Dust accumulation on leaves also increases absorption of infrared radiation (Eller 1977), reducing leaf respiration, photosynthesis, and growth (Saunders 1971).

Bryophytes and lichens were found to be less abundant near the Dalton Highway in other studies (Spatt and Miller 1981, Walker and Everett 1987). Nonvascular taxa may be especially vulnerable to dust disturbance, due to structural characteristics that make them susceptible to the disturbance effects of atmospheric pollutants (Rao 1982). Bryophytes and lichens absorb moisture and dissolved nutrients directly through their cell walls (Hale 1974, Scagel et al. 1984). Excess moisture from accumulated snow or ponding from road blockage may lead to saturation of the lichen thalli, reduced rates of gaseous diffusion through the thallus to the algal layer, and decreased photosynthesis (Hale 1974). Dust may also absorb water through noncutinized leaf surfaces, increasing evaporation, and a dust coating may physically restrict gas exchange and attenuate photosynthetically active light, all reducing production (Spatt and Miller 1981). Furthermore, lichen susceptibility to atmospheric pollution may be enhanced by an efficient mechanism for accumulating toxic levels of minerals (Hale 1974), and possibly absorbing excessive and harmful levels of minerals from chronic dust deposition. In addition, environmental pH appears to affect different lichen associations (Gilbert 1976), and although wide ranges of pH have been found to be tolerated by lichen phycobionts (algal components), the mycobiont (fungal component) of most lichens appears to depend significantly on the pH of the cultural medium (Hale 1974). Bryophyte distribution is also influenced by pH (Robinson et al. 1989).

Moss cover at Sagwon was less affected by the presence of high dust loads. The moss *Tomentypnum nitens*, normally dominant in nonacidic tussock tundra (Walker et al. 1994), showed virtually no difference in cover with respect to the road disturbance and does not appear to be greatly affected by the slight increase in pH near the road in normally nonacidic tundra. However, the moss species *Limprichtia revolvens*, a species that dominates in extreme-rich fens (mean pH \approx 7.5) and

moderate-rich fens (mean pH \approx 6.5) (Vitt 1990), increased near the road. Soil pH near the road at Sagwon averaged \approx 7.1, compared to 6.5 in undisturbed sites. This slight increase in pH may be enough to provide more suitable conditions for the growth of *L. revolvens* (Robinson et al. 1989). At Prudhoe Bay, Alaska, where higher dust loads occur, however, even minerotrophic mosses such as *Tomentypnum nitens*, *Drepanocladus brevifolius*, and *Limprichtia revolvens* were eliminated near the road (Walker and Everett 1987). The feather moss *Hylocomium splendens* also had less cover near the road at Sagwon. The growth of many feather mosses is controlled by rainfall frequency and degree of protection from evaporation stress (Busby et al. 1978). Near the road, warm soil and dusty air may provide conditions that are too stressful for this moss to be productive.

Most of the changes in bryophyte composition at Toolik are probably due to the change in soil pH, but different bryophyte species were most abundant at specific distances from the road, likely due to a combination of several other additional factors. Controlled experiments where selected species are physically removed from the plant canopy would help examine the causes of these patterns, since competition and individual ability of species to thrive on the altered habitat can determine increased or decreased presence. Weedy species of mosses such as *Bryum wrightii* and *Certodon purpureus* are likely responding to the new mineral substrates near the road (Steele 1978, Crum and Anderson 1981, Vitt et al. 1988). *Aulacomnium turgidum* and *Dicranum* spp. had high abundance at intermediate distances from the road and may be responding positively to the decreased competition from *Sphagnum*. Although the moss *A. turgidum* normally occurs with some abundance in acidic tussock tundra (Walker et al. 1994), this species has been found to prefer a calcareous habitat (Vitt et al. 1988) and may be responding to the increase in soil pH (Walker and Everett 1987). Mosses may outcompete vascular species for surface-applied ^{15}N (Marion et al. 1987), and so *A. turgidum* and *Dicranum* spp. may also be benefitting from minerals added by the road dust. Furthermore, overall bryophyte phytomass responds consistently to the gradient of hydrological conditions at a given locality (Vitt and Pakarinen 1977). *Dicranum* normally thrives in an intermediate soil moisture regime and *Sphagnum* normally is found in very moist areas (Alpert and Oechel 1982). These mosses may be responding to the altered soil moisture. It is unknown whether the *Polytrichum* is responding to dust disturbance or to a local difference in substrate.

Sphagnum productivity was lower near the road than farther away in 1978 (Spatt and Miller 1981). *Sphagnum* is intolerant to calcium and high pH levels and grows only in habitats with sufficient water supply (Clymo 1973, Spatt and Miller 1981, Clymo and Hayward 1982, Brown 1988). The acidic organic soils at

Toolik, derived from *Sphagnum* peat, are particularly susceptible to pH change from the road dust. Normally, conditions created by *Sphagnum* produce a positive feedback to the system, and peat accumulation occurs. But the dust-induced increases in pH make conditions unsuitable for *Sphagnum* growth. The interaction of acidic tundra vegetation, soil formation, and permafrost maintenance is then altered and replaced by an anthropogenically controlled disturbance community. Although alkaline conditions, such as those at Sagwon, are found naturally in some organic soils under the influence of loess (Walker and Everett 1991), anthropogenically introduced alkalinity by road dust alters the balance of the acidic tundra ecosystem.

CONCLUSIONS

Effects on substrate properties.—(1) Soil pH was higher near the road. Acidic tundra soils are particularly altered by the addition of calcareous road dust. (2) Availability of soil nutrients NO₃-N and P was lower next to the road. The differences may be due to a change to coarser grained mineral soils next to the road altering the cation exchange capacity or to the increased nutrient uptake by vegetation that has been altered in composition near the road. (3) Active-layer thaw was deeper near the road, likely due to a combined result of several factors that have affected the permafrost. The snowbank that forms next to the road provides more insulation in the winter, and dust-induced early snow meltout provides more cumulative radiation absorption by the permafrost through a longer growing season. Greater soil bulk density provides greater heat conductivity, and species composition changes result in a reduction of an insulative moss mat.

Effects on vegetation biomass.—(1) Total biomass was lower next to the road in both nonacidic and acidic tundra, despite higher graminoid biomass near the road in both tundra types and higher deciduous shrub biomass in nonacidic tundra. (2) Mosses were negatively affected by the road disturbance, particularly in acidic tundra where there is virtually no moss biomass next to the road. The normal dominant moss of acidic tundra, *Sphagnum*, is unable to produce in the altered conditions near the road, particularly due to heavy dusting and increased pH.

Effects on vegetation species composition.—(1) Species composition was different next to the road compared with undisturbed areas, and species richness was lower, particularly in acidic tundra. Though the alteration of community structure is undoubtedly due to both abiotic factors (including change to substrate properties next to the road) and biotic factors (including competition), it is difficult to determine exact causes of change. Controlled experiments could clarify matters. (2) Graminoids, mostly *Eriophorum vaginatum*, are more abundant next to the road. *E. vaginatum* is known to be successful in disturbed conditions. (3) Deciduous shrub cover is increased next to the road at

the nonacidic tundra site, and *Salix lanata* ssp. *richardsonii* may be especially adaptable to road-altered conditions. (4) Lichens are reduced in abundance next to the road in both acidic and nonacidic tundra. Growth-form characteristics make lichens susceptible to the road and dust disturbance. (5) Mosses of the two tundra types were differentially affected. Cover of the dominant moss of nonacidic arctic tussock tundra, *Tomentypnum nitens*, is virtually equal at all distances from the road in nonacidic tundra and did not appear to be affected by road disturbance. *Sphagnum*, normally dominant in acidic tundra, simply cannot grow in disturbance conditions created near the road. Other mosses in acidic tundra occur with unusually high cover at intervals with increasing distances from the road. The mosses may be responding positively to a variety of factors including changes in pH, moisture, nutrients, and change in competitive regime due to a decrease in cover of other species. Species affected include weedy mosses (*Bryum* spp., *Ceratodon purpureus*, and *Tortula ruralis*), and mosses *Aulacomnium turgidum*, *Dicranum* spp., *Sphagnum* spp., and *Polytrichum juniperinum*.

Road dust and development can potentially greatly affect large regions of tundra, particularly in areas with dense road networks. This has already occurred at Prudhoe Bay, Alaska, where extensive thermokarsting has affected adjacent landscapes along heavily travelled roads (Walker and Everett 1987). In northwestern Siberia, damage caused by development in tundra areas is even greater due to sandy aeolian substrates that are easily remobilized if disturbed, presenting a critical threat to the indigenous Nenets population and their pastoralist economy (Forbes, *in press*). The Dalton Highway was previously restricted by permitting, but was opened to the public in 1994. Increased usage of this road is expected. Only dust abatement procedures may retard damage in already developed areas or in areas with projected increased usage.

In areas of projected development, it would be useful instead to first identify tundra that has high susceptibility to disturbance by roads and dust (Walker and Everett 1987). This paper demonstrates that nonacidic and acidic tundra are differentially affected. Efforts to avoid road construction in areas of acidic tundra, through deliberate prior planning, would help minimize negative ecosystem effects in areas of proposed oil or gas exploration and development in the circumpolar, such as the Arctic National Wildlife Refuge (ANWR). Terrain characteristics and ground ice content are already routinely considered in road construction plans in the Arctic (Brown 1980), but more comprehensive procedures would include sensitivity maps based on information about vegetation composition and substrate. Two satellite-imagery-based maps report similar estimates of vegetation cover in ANWR: 26.5% nonacidic, 28.5% acidic tundra in Walker et al. (1982) and 24% nonacidic, 35% acidic tundra in Jorgenson et al. (1994). Vegetation of the Kuparuk River watershed in

northern Alaska is estimated to be 38.9% nonacidic and 30.8% acidic tundra (D. A. Walker and N. Auerbach, *unpublished manuscript*). Vegetation maps such as these should be used to facilitate decision-making.

In summary, although both nonacidic and acidic tundra are affected by road and dust disturbance, we found that acidic tundra is particularly vulnerable. The consequences of development could be reduced if suitable guidelines addressing the detrimental effects of road and dust disturbance were implemented.

ACKNOWLEDGMENTS

Funding for this project was provided by the Department of Energy's R4D Program (Response, Resistance, and Resilience to, and Recovery from Disturbance in Arctic Ecosystems) Grant Number DE-FG02-84ER6042.A006, the University of Colorado Museum Walker Van Riper Fund, and the National Science Foundation ARCSS-LAII Program (Arctic System Science—Land, Atmosphere and Ice Interactions) Grant Number OPP-9415554. We thank John Dietz for field assistance, and Scott Randolph for assistance in figure preparation. Dust composition analysis by Richard Cashwell at the Nuclear Reactor Laboratory, University of Wisconsin, was provided by the Department of Energy Reactor Sharing Program. Soil analysis was done by Colorado State University Soil Testing Laboratory, Fort Collins. Verification of *Sphagnum* samples and identification of the remainder of the mosses not identified in the field at both sites were by Dr. Dale Vitt, Department of Botany, University of Alberta, Edmonton, Alberta, Canada. We thank our reviewers for their helpful comments.

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