Parent material depth controls ecosystem composition and function on a riverside terrace in northwestern Alaska[1]

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Abstract: Many studies have focused on factors that influence ecosystem composition and function, but little is known about the influence of varying quantities of a single parent material without confounding effects of age or location. On a riverside terrace of the Agashashok River, the depth of the cap of silt and sand over the gravel floodplain strongly influenced species composition, production, and response to additions of nitrogen (N) and water. Thin siltcaps (< 0.25 m) had vegetation dominated by herbaceous species, whereas thicker siltcaps had a strong component of shrubs. The depth of the siltcap accounted for about 50% of the variation in the first principle-component of the variation in species composition and cover. *In situ* net N mineralization increased with increasing siltcap depth, but net nitrification declined. Production by herbs increased by about 20% with water additions but not with N additions, and the responses were strongest at the two intermediate siltcap depths. Shrub production increased by about 30% with N addition but not with water additions, with stronger responses on thicker siltcaps. The importance of the quantity of parent material may apply to other situations where the depth of fine-textured parent material is relatively shallow. Greater attention to the role of quantitative differences in parent material appears warranted.
Keywords: arctic ecosystems, productivity, biomass, nitrogen mineralization, nitrification, nutrient limitation, water limitation, *Salix spp., Betula nana, Dryas octopetala.*

Résumé: De nombreuses études ont permis de se pencher sur les facteurs influençant la composition et le fonctionnement des écosystèmes, mais on connaît bien peu l'influence de l'épaisseur variable d'un type donné de matériel originel, sans une certaine confusion avec l'effet de l'âge ou de la localisation. Sur une terrasse alluviale bordant la rivière Agashashok, l'épaisseur du revêtement de limon et de sable au-dessus du gravier constituant la plaine inondable influence grandement la composition floristique, la production ainsi que la réaction de la végétation à l'apport en azote et en eau. Un couvert végétal à prédominance herbacée apparaît sur les revêtements limoneux de faible épaisseur (< 0.25 m), alors que les revêtements plus épais ont une forte composante arbustive. La profondeur du revêtement de limon rend compte de 50 % de la variance dans l'analyse des facteurs principaux d'ordre un, relatifs à la composition floristique et au recouvrement. La minéralisation nette de l'azote (N) augmente avec un accroissement de l'épaisseur de limon, mais la nitrification nette diminue. La production des plantes herbacées a augmenté d'environ 20 % par suite d'un apport en eau, non pas d'un apport en azote, les réactions les plus fortes étant apparues là où le revêtement limoneux se situait dans les deux classes intermédiaires d'épaisseur. La production des arbustes a augmenté d'environ 30 % par suite d'un apport en azote, non pas d'un apport en eau, les réactions les plus fortes ayant été obtenues sur les revêtements limoneux les plus épais. L'épaisseur du matériel originel peut s'avérer tout aussi importante dans d'autres situations où le matériel à texture fine reste relativement mince. Il pourrait être opportun d'accorder une attention plus grande au rôle que peuvent jouer des différences dans l'épaisseur du matériel originel.
Mots-clés: écosystèmes arctiques, productivité, biomasse, minéralisation de l'azote, nitrification, limites nutritives, limites en eau, *Salix spp., Betula nana, Dryas octopetala.*

Introduction

The state factor approach (Jenny, 1980) has been a productive framework for examining the components of ecosystem development (Van Cleve *et al.*, 1991). Classic studies in Alaska have examined the roles of time and species in ecosystem development (Crocker & Major, 1955; Crocker & Dickson, 1957; Bliss & Cantlon, 1957; Van Cleve *et al.*, 1986; 1993; Walker & Chapin, 1986; Bormann & Sidle, 1990), and some work has begun to characterize the influence of topography on ecosystem composition and function (Giblin *et al.*, 1991; Nadelhoffer *et al.*, 1991; Van Cleve *et al.*, 1991; Valentine & Binkley, 1992). Classic studies of the role of parent material on the development of soils and ecosystems have focused on types of parent

materials (Buol, Hole & McCracken, 1980; Jenny, 1980; Birkeland, 1984). We know of no studies that have explored the effects of the quantity of a single parent material on ecosystem composition, structure, and function. How different would an ecosystem be that developed on a 0.2-m deep layer of fine mineral material from one that developed on a 0.5-m layer of the same material? One impediment to such studies is that differences in parent material are often confounded with other state factors such as topographic position (*e.g.* midslope *versus* lower slope), age (multiple deposition events), or location (with microenvironmental differences).

In this study, we examined an array of ecosystems on a single riverside terrace in northwestern Alaska. We examined relationships between the thickness of the silt/sand cap

(atop gravel deposits) and species composition, vegetation structure, soil N mineralization, and water and nitrogen limitations on growth.

Site description and methods

The study site was located beside the Agashashok River (67° 28' N, 162° 14' W), a tributary of the Noatak River, about 80 km north of Kotzebue, Alaska, at the western end of the Baird Mountains of the Brooks Range (Binkley *et al.*, 1994). No long-term weather records are available for this site, but precipitation probably averages about 500 mm/year with a mean annual temperature of about -7°C (based on records for Kobuk, about 200 km to the southeast; Patric & Black, 1968). For the growing season of 1992, mean monthly air temperatures (shaded box at 1.5 m height) at our Agashashok site were 14°C (June), 12°C (July), 8°C (August) and 2°C (September). In July, incident solar radiation averaged about 12.5 MJ m^{-2} day^{-1}.

Large gravel beds form the base of the floodplain, and some terraces are capped with a layer of silt and sand of varying depth. The slope of the gravel beds is relatively steep in response to high water velocities. The silt and sand caps, deposited during flood events, are more level. The riverwater is extremely clear at low flows, but turbid during stormflows. We established our plots on a 500-m span of a gravel terrace capped with a single silt/sand layer that varied in depth from < 0.01 m at the upstream end to > 0.6 m at the downstream end. The width of the terrace ranged from about 20 m at the upstream end, to > 100 m at the downstream end. The terrace is about 2.5 m above the current river channel at the upstream end, and 1.5 m above the current channel at the downstream end. This difference in height above the river results from the slope of the river in the cobblestones of the valley bottom; the surface of the terrace is level, as expected for a flood deposit of fine textured material. The vegetation at the upstream, thin-siltcap end of the terrace is dominated by *Dryas octopetala* and other herbs. With increasing siltcap depth, the vegetation shifts to greater dominance by shrubs of *Salix* (primarily *S. alaxensis*, *S. hastata*, and *S. lanata*), *Betula nana*, and *Potentilla fruticosa* (nomenclature after Hultén, 1968). Erosion along the current river channel provided excellent views of the gradation of siltcap thickness and the distributions of roots; no roots were observed penetrating into the gravel beneath the siltcaps. Scattered saplings and trees of white spruce (*Picea glauca*) are found throughout the terrace, on both thin and thick siltcap portions. The texture of the siltcap is primarily very-fine sandy loam, ranging from 45 to 55% sand, 40 to 50% silt, and about 5% clay (by the hydrometer method 15-5, Gee & Bauder, 1986), with no trend along the terrace or with siltcap depth. No soil horizon development is apparent, and we found no evidence of buried soil horizons. We could not establish the age of the siltcap deposit, but isolated white spruce on the terrace are up to 200 years old, providing a minimum age.

In the summer of 1991, two series of plots were established along the terrace. The first series described the vegetation in relation to siltcap depth, and the second series manipulated the supplies of nitrogen (N) and water. The descriptive series consisted of twenty-two 2 m × 2 m plots,

every 20 m along a 440-m transect (parallel to the river, about 5 to 10 m from the current channel). These plots spanned a range of siltcap depths from 0.08 to 0.68 m. At each plot, the depth of the siltcap was measured (with a soil auger in the center of each plot), and species composition and cover (visual estimates in quadrat frames) were recorded. In the summer of 1993, soil cores (100 mm diameter, 100 mm deep) were incubated in thin plastic bags to determine net soil N mineralization and nitrification (Binkley & Hart, 1989). Two cores were collected from each of the 22 plots and extracted on June 28, and two additional cores were placed in plastic bags and replaced in the soil to incubate until August 8. At each time, the two cores/plot were composited and a 10-g (fresh weight) subsample was extracted with 100 mL of 2 M KCl and filtered within 2 hours of collection. The extracts were returned to Colorado and stored frozen for 4 months until analysis of ammonium-N and nitrate-N on a Lachat Automated Flow system. All values are reported on an oven-dry soil basis. The net difference in nitrate concentrations between the initial and post-incubation samples is net nitrification, and the net difference between initial and post-incubation ammonium + nitrate concentrations is net mineralization. These net values probably do not represent the real rates of N supply to plants, but they may serve as an index (Binkley & Hart 1989).

The second, manipulated series of plots consisted of 4 arrays placed along the original transect, with siltcap depths of 0.08, 0.16, 0.39, and 0.34 m. The coefficient of variation in depth within each array was about 15%, based on 6 points/array. Each of the four arrays contained sixteen 2 m × 2 m plots (64 plots total), with a 1-m buffer strip separating the plots. Four treatments were replicated 4 times in a completely randomized arrangement: control; +N (15 g-N/m^2 as ammonium nitrate on July 20, 1991), +water (each plot irrigated with 40 L [= 10 mm] of riverwater on July 21 and August 5, 1991, and July 22 and 28, 1992), and +N+water. The species composition and percent cover were recorded for each plot. To determine the treatment effect on the production of herbs, all herbs were clipped from each plot late in the growing season before senescence (August 6, 1991), and then late in the next growing season (August 5 to 15, 1992). Shrub production was assessed by painting a small dot 10 mm below the terminal bud on a subset of twigs on each species in each plot in August of 1991. In August of 1992, the twigs were clipped 10 mm above the dots and weighed. Multiplication by the number of twigs per species and plot provided an index of shrub production (radial increments in stem biomass were not included). Nitrogen use was calculated as the N concentration (Kjehldahl digest in H_2O_2 and H_2SO_4, colorimetry using a Lachat Continuous Flow Analyzer) times production. Some of this N would have come from storage pools within the plants, and some from current-year uptake from the soil.

Vegetation composition was analyzed in the descriptive series of plots by principal components analysis (PCA), with the percent cover of each of 22 plant species (or groups) in the 22 plots (in SYSTAT 5.0, FACTOR routine, Wilinson, 1991). We lumped *Salix spp.*, and graminoids, because of incomplete species identification. The PCA scores for the first axis were then used as a dependent

variable in a regression with siltcap depth as the independent variable. Similarly, the net mineralization rates were regressed against siltcap depth.

The experimental array series was analyzed using production and N use of herbaceous and shrubby vegetation as dependent variables, and treatments (control, +N, +water, +N+water) as class variables in an ANOVA (SYSTAT 5.0, MGLH, Wilkinson, 1991).

Results and discussion

Species composition changed dramatically along the transect (Table I). The first PCA axis accounted for 38% of the total variation in species composition and cover among the 22 plots, and the siltcap depth accounted for 51% ($p <$ 0.0001, Figure 1) of the variation in the first PCA axis. In general, siltcaps < 0.25 m thick had similar plant communities (similar PCA scores), whereas siltcaps > 0.25 m had a wider range of species composition (at a scale of 4 m²). Net nitrogen mineralization also increased with depth of the siltcap (Figure 2; $r^2 = 0.26$, $p < 0.02$), but net nitrification surprisingly declined substantially with siltcap depth ($r^2 = 0.45$, $p < 0.001$). This pattern could result from declines in gross nitrification rates along the siltcap sequence, resulting from greater competition between nitrifiers and heterotrophic microbes and plants. Alternatively, lower net nitrification could result from higher microbial immobilization of nitrate in deeper soils where C availability may be higher (Hart *et al.*, 1994). In an earlier study near the shallow siltcap arrays, Binkley *et al.* (1994) found that microbial immobilization of both ammonium and nitrate was more sensitive to temperature and moisture regimes than were the gross rates of mineralization or nitrification.
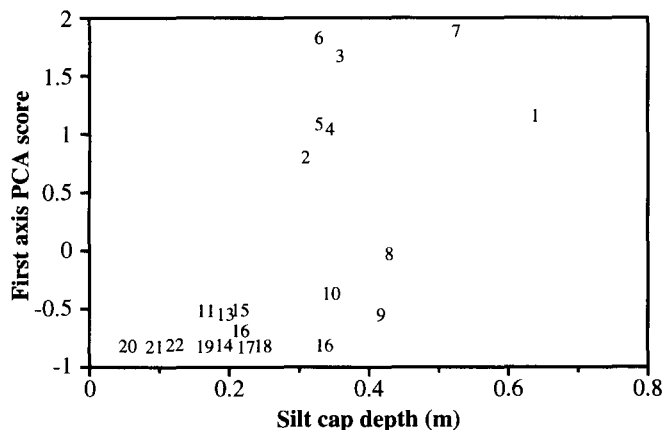

FIGURE 1. First-axis PCA score as a function of the thickness of the siltcap. Numerals represent plots at 20-m intervals starting on the downstream, thick-siltcap end of the transect. Siltcap depth account for 51% of the variation in the $\log_e$ of the PCA score.

The depth of siltcap in the manipulated arrays also influenced species composition and biomass production of both herbs and shrubs ($p < 0.001$; Table II). Irrigation significantly ($p = 0.007$) increased herbaceous biomass, but N fertilization did not ($p = 0.13$; Figure 3). Conversely, N fertilization substantially increased shrub production ($p = 0.06$), but water did not ($p = 0.51$). The combination of these opposite patterns produced significant responses in

TABLE I. Species cover (%) for 2 m × 2 m plots (species nomenclature from Hultén, 1968)

| Species / Plot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Silt/sand depth (m)	0.65	0.32	0.37	0.35	0.34	0.34	0.54	0.44	0.43	0.36	0.18	0.23	0.21	0.19	0.23	0.35	0.24	0.26	0.18	0.07	0.11	0.14
Salix spp.	2	20	31	12	2	12	10	7	3	0.5	0	0.5	5	0	0	1	1	2	8	0	0	0
Picea glauca	0.1	0	0.1	0.1	35	0.1	0	12	16	5	0.1	0	0.1	0.1	7	7	0	0	0	0	0	0
Potentilla fruticosa	14	1	8	4	0.5	3	3	9	5	5	42	20	35	2	5	17	12	10	0	0	3	2
Dryas octopetala	0	0.5	2	28	23	11	0.1	20	30	27	1	8	5	15	10	5	10	25	55	55	45	22
Graminoid	20	5	9	3	3	6	6	4	6	5	4	7	8	2	8	5	8	10	1	0.5	2	6
Oxytropis campestris	0	0.5	1	2	0.5	0	0	5	0	6	1	0	0	1	0.5	2	3	0.5	13	6	5	0
Shepherdia canadensis	3	2	12	0	0.1	0.1	9	4	1	1	4	0	8	0	0.1	0.1	0	1	0	1	1	0.1
Arctostaphylos rubra	4	0.5	9	0.5	0	1	2	0.1	0.1	0.5	0	0.5	0	0	0	2	4	5	0.5	0	2	2
Betula nana	1	9	0	0	1	0.1	13	4	7	0	0.5	1	1	2	2	1	0	3	0	0	0.1	0
Senecio spp.	0.5	2	0.1	1	1	0.1	0.5	0.5	0	0.1	0	0	1	6	0.1	0	0.5	0	1	0.1	0	1
Epilobium latifolium	0	0	0	0	0	0	0	0.1	0.1	0	0.5	1	0.5	0.5	1	0	1	0	0	0	0	0
Zygadenus elegans	0.5	0.5	0	1	1	0.5	0.1	0	0.5	0	1	0	0	0.5	0	0.5	0	0.5	0	0	0.5	0.5
Sanguisorba officinalis	1	0.1	0.5	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0.1	0	0.1
Hedysarum alpinum	0.5	2	3	1	1	3	4	2	1	1	0	0	0	0.1	1	2	4	1	0	0	0.1	1
Anemone parviflora	1	0.5	1	0.5	1	3	1	1	0.1	2	0.1	0.1	0	0.1	0	2	1	0.1	0.5	0	1	1
Vaccinium uliginosum	0	0	0.1	0	0	0	0	0.5	0	0.1	0	0	0	0	0	0.1	0	0	0	0	0	0
Parnassia palustris	0.5	0	0	0	0	0.1	0	0	0.1	0.1	0	0	0	0.1	0	0	0	0	0.5	0	0.1	0
Cypripedium passerinum	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platanthera obtusata	0.1	0	0	0.1	0.1	0	0	0	0	0	0.5	0	0	0	0.1	0	0	0	0	0	0.1	0
Tofieldia pusilla	0.5	0.5	0.5	0	0	0	0	0.5	0.5	0.5	0	0	0	0	0	1	0	0	0	0	0.1	0.5
Pedicularis verticillata	0	0	0.2	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Equisetum spp.	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
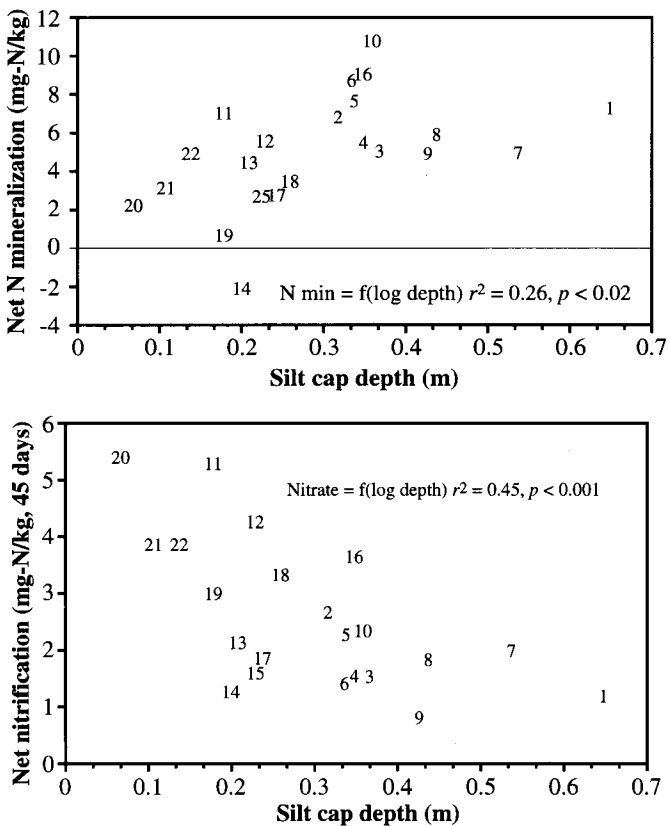
FIGURE 2. *In situ* (45 days) net nitrogen mineralization (upper) and net nitrification (lower) as functions of the thickness of the siltcap. Numerals represent plots at 20 m intervals starting on the downstream, thick-siltcap end of the transect.

total vegetation production to both treatments (N: $p = 0.01$; water: $p = 0.003$). No interactions between the two treatments were significant, but both showed significant interactions with siltcap depth. For example N fertilization increased shrub production by more than 50% on the thicker
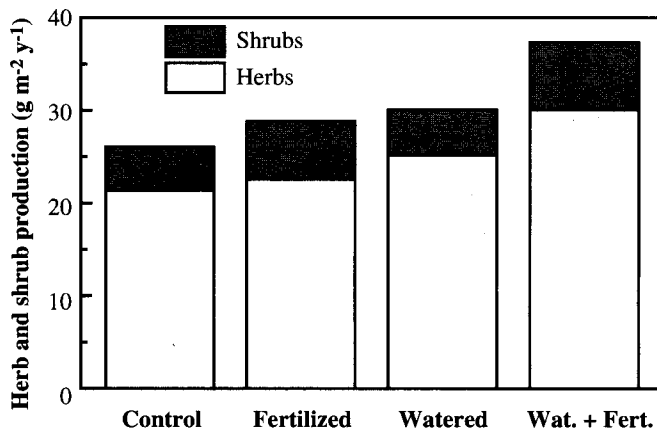

FIGURE 3. Overall treatment means for herb and shrub production in response to additions of nitrogen and water. Irrigation significantly increased production of herbs but not shrubs, whereas fertilization increased production of shrubs but not herbs.

siltcap sites (0.34 and 0.39-m thick), but not on the thinner (0.08 and 0.16-m thick) siltcap sites. Interestingly, the higher N supply rates on the thicker-siltcap portions of the terrace were associated with the greater response of shrub production to addition of N. The limitation of N supply on production was not a simple function of N supply rate.

Nitrogen use in control plots did not differ significantly among the arrays (Table III). However, addition of N or water significantly increased N use by herbs, and by herbs+shrubs, but not by shrubs alone. The N uptake response to these treatments also tended to be higher on the arrays with the deeper siltcaps, but these interactions were not significant (N × depth: $p = 0.11$, water × depth: $p = 0.13$). Addition of N (but not of water) significantly increased N concentrations in current year tissues, and therefore fertilization reduced the N use efficiency (production/N use).

The terrace in our study may be unusual in providing a

TABLE II. Mean and standard deviation (SD) of percent species cover ($n = 16$, 2 m × 2 m plots/array) for species with > 0.5% average cover on any array

Species	Array 1		Array 2		Array 3		Array 4	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Salix spp.	2.06	(2.06)	1.81	(1.51)	17.2	(10.9)	13.1	(7.74)
Picea glauca	0.31	(1.08)	0.50	(0.94)	2.44	(4.54)	1.63	(3.39)
Potentilla fruticosa	0.06	(0.27)	2.63	(2.52)	9.13	(4.78)	9.31	(4.45)
Dryas octopetala	45.4	16.2)	33.3	(14.5)	8.38	(7.30)	5.69	(4.90)
Oxytropis campestris	1.69	(0.93)	3.50	(1.97)	0.75	(0.66)	0.06	(0.24)
Shepherdia canadensis	0.31	(0.62)	0.81	(0.73)	1.06	(0.97)	1.00	(1.17)
Salix reticulata	0.00	(0.00)	0.06	(0.24)	2.75	(3.63)	2.13	(2.09)
Arctostaphylos rubra	0.13	(0.00)	0.69	(0.77)	2.44	(2.78)	0.56	(0.79)
Betula nana	0.00	(0.00)	0.00	(0.00)	0.56	(1.06)	0.19	(0.73)
Senecio spp.	0.13	(0.36)	2.31	(1.16)	0.94	(1.92)	0.69	(0.68)
Epilobium latifolium	1.19	(1.64)	0.25	(0.75)	0.06	(0.24)	0.13	(0.48)
Zygedenus elegans	0.13	(0.53)	0.94	(1.03)	0.44	(0.50)	0.13	(0.48)
Sanguisorba officinalis	0.00	(0.00)	0.00	(0.00)	0.38	(0.70)	1.44	(1.41)
Hedysarum alpinum	0.00	(0.00)	0.13	(0.33)	4.00	(1.84)	3.13	(1.76)
Anemone parviflora	0.13	(0.53)	0.44	(0.79)	1.19	(1.24)	0.81	(1.13)
Vaccinium uliginosum	0.00	(0.00)	0.00	(0.00)	0.56	(1.17)	0.13	(0.48)
Cypripedium passerinum	0.00	(0.00)	0.00	(0.00)	0.06	(0.24)	0.25	(0.43)
Galium boreale	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.19	(0.53)
Pinguicula villosa	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.06	(0.24)
Tofieldia pusilla	0.00	(0.00)	0.13	(0.48)	0.19	(0.39)	0.00	(0.00)
Pedicularis verticillata	0.00	(0.00)	0.00	(0.00)	0.19	(0.06)	0.06	(0.24)

TABLE III. N use (mg/m²) by treatment. N use is N concentration times biomass of current year shrub twigs+leaves and herbs. Means followed by the same letter (within columns) do not differ at $p = 0.1$

Treatment	Herbs	Shrubs	Total
Control	0.88 (0.32)a	0.44 (0.25)a	1.31 (0.24)a
+N	1.06 (0.37)b	0.88 (0.25)a	1.94 (0.32)b
+Water	0.82 (0.24)a	0.47 (0.13)a	1.29 (0.13)a
+N+water	1.68 (0.55)b	0.54 (0.72)a	2.22 (0.58)b

gradient of depth of a surface deposit overtop an ecologically inactive bed of gravel. This unusual setting, however, allowed the effects of the quantity of parent material to be identified and manipulated. With siltcap depths of less than about 0.25 m, species composition varied little (based on similar first-axis PCA scores), N supply was low, and the herb-dominated communities showed little response to addition of N but a strong response to water. Greater depths of the siltcap revealed more variable community composition (a wider range of first-axis PCA scores), higher N supply, and greater responsiveness of the vegetation to addition of N. We have no information on the likely development of these ecosystems over time; we observed no signs (such as recruitment of seedlings of shrubs or spruce) that suggested any successional trends on this terrace. The limitations imposed by the quantity of parent material will probably insure that the ecosystems along this terrace will not converge in species composition. Our findings regarding the quantity of parent material may apply to other situations where the depth of soil parent material is relatively thin. The quantity of parent material may also be critical in situations where gravel and rock content is high and variable (such as colluvium or talus). Greater attention is warranted on the role of quantitative differences in parent material on ecosystem composition, function, and response.

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