



# Changes in soils along a vegetational (altitudinal) gradient of the northern Rocky Mountains

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CHANGES IN SOILS  
ALONG A VEGETATION-ALTITUDINAL GRADIENT  
OF THE NORTHERN ROCKY MOUNTAINS <sup>2</sup>

T. Weaver<sup>1</sup>

As one moves from the warm dry plains of eastern Montana to the cool moist peaks of the northern Rocky Mountains he might pass through a series of native vegetation types: *Bouteloua gracilis*, *Agropyron spicatum*, *Festuca idahoensis*, and *Festuca scabrella* grasslands; *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Abies lasiocarpa* forests; and alpine tundra (Kuchler 1964, Muggler and Handl 1974, Pfister *et al.* 1977).

It is commonly observed that when one moves up a vegetational gradient he moves up a soils gradient (e.g. Eyre 1963, Whittaker *et al.* 1968, Hanawalt and Whittaker 1976 and 1977). In the northern Rocky Mountains, Thorp (1931, N Wyoming) observed that organic matter increased, that pH decreased, that the depth to free lime increased and that the thickness of A- and B-horizons increased as he moved up a vegetational gradient similar to that described above. The same trends, as well as a tendency for nutrients to become most available at the grassland-forest boundary, were observed along a similar vegetation gradient in British Columbia (Spilsbury and Tisdale 1944). Such trends correlate well with broad groups in the 1938 Soil Taxonomy (Agricultural Experiment Station 1964 and Nimlos 1963) as well as in the 1977 Soil Taxonomy (Weaver 1978).

The objects of this paper are 1) to describe the change in soils observed along this gradient in more detail, 2) to consider their genesis briefly, and 3) to consider their importance to plants.

METHODS

Previously analyzed soils representative of northern Rocky Mountain vegetation series were sought. One non-limestone alpine soil of Montana (Nimlos and McConnell 1965, cf Retzer 1956) and forty-eight benchmark soils

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broadly representing soil series dominated by the subalpine vegetation series were found. The latter soils have been studied in the field by University and USDA Soil Conservation Service personnel and analyzed by the SCS National Soil Survey Laboratory, Lincoln, Nebraska. Organic matter was measured colorimetrically after dichromate oxidation; total nitrogen was measured with a Kjeldahl method; potassium, calcium, and magnesium were extracted with 1 M ammonium acetate and determined by atomic absorption, and pH was measured on a 1:1 soil-water paste (USDA 1972). Relevant data are available through the Montana Soil Data system (Decker *et al.* 1975).

The soil series associated with each climax vegetation series (and the number of samples of each) are listed below: *Tundra* series, Ptarmigan (1); *Abies lasiocarpa* series, Holloway (1); *Pseudotsuga menziesii* series, Greenough (2), Loberg (2), and Yourame (1); *Pinus ponderosa* series, Bass (1), Charlos (1), Gorus (2), Somers (1), and Tarkio (2); *Festuca scabrella* series, McDonald (3), and Teton (1); *Festuca idahoensis* series, Alder (1), Gaylord (1), Haccke (1), Melville (2), Phillipsburg (3), and Sweetgrass (3); *Agropyron spicatum* series, Absarokee (2), and Martinsdale (2); and *Bouteloua gracilis* series, Danvers (5), Hopley (3), and Nunn (7). Benchmark soils data may be biased toward widespread and agriculturally important soils.

Average characteristics (with their standard errors) were calculated for three horizons (top 10 cm, A, and B) of the soils of each of the six vegetational series represented by four or more benchmark soils. Prior to these calculations were summary calculations in which subhorizons were pooled with weighted averages; for example, nitrogen contents of an A<sub>11</sub> and an A<sub>12</sub> horizon might have been averaged to provide a single value for the A-horizon.

The capacity of typical (average) soils at field capacity to provide water to plants was calculated for each vegetation type by the following methods. The volume of the soil beneath one square centimeter of surface was calculated by multiplying 1 cm<sup>2</sup> by the soil layer thickness (depth) by the percentage of soil in that layer (100 minus percent stone on a volume basis in that layer). The weight of the soil was calculated by multiplying its volume by the soil's bulk density. The quantity of water the soil could supply to plants was calculated as soil weight times (water holding capacity at field capacity (1/3 bar) minus water holding capacity at permanent wilting point (15 bar)); since 1/3 bar water was not measured for many of our soils it was estimated as twice 15 bar water (Decker 1972). Since a gram of water occupies 1 cubic centimeter the resultant figures express available water holding capacity in centimeters.

Quantities of available organic carbon, nitrogen, potassium, calcium, and magnesium in typical soils of each vegetation series were calculated similarly. The weight of soil subtending a one square centimeter area was found by multiplying surface area (1 cm<sup>2</sup>) x soil layer thickness (cm) x (100 minus percent stone) x bulk density (gm/cm<sup>3</sup>). The quantity of available nutrient was found by multiplying this soil weight by the percent of total soil weight the nutrient comprised. Available nutrients in gm/cm<sup>2</sup> were converted to metric tons/ha by multiplying by (100 million cm<sup>2</sup>/ha)/(1 million gm/ton). For monovalent ions (K) milliequivalents/100 gms were converted to percent by multiplying gms/mole x 1/1000 x meq/100 gm; for divalent ions

(Ca and Mg) "x 1/2" was added to this formula. Organic carbon is converted to organic matter by multiplying by 1.7 (Allison 1965).

## RESULTS AND DISCUSSION

**Physical and chemical characteristics.** The thickness of solum (A- and B-horizons) increases from 0.5 M in dry grasslands to 1 M in *Festuca* grasslands and lower forests to 2 M in *Abies lasiocarpa* forests (Tables 1 and 3). This trend is expected since increasingly moist climates (i.e., more precipitation and lower evaporation rates) provide for deeper weathering. The trend does not extend into the alpine (Retzer 1956, Nimlos and McConnell 1965) either because the surfaces are too new or because temperatures are too low.

Percentages of coarse materials in the solum increase as one moves from dry grasslands to high forests (Table 1). Stone is nearly absent from dry *Bouteloua* and *Agropyron* grasslands, occupies less than 10% of the profile in *Festuca* grasslands and *Pinus* forests, and occupies 15-50% of soil profiles in higher forests and tundra. Sand comprises about 30% of the soil in most grasslands (cf *Agropyron*) and *Pinus* forests and becomes increasingly important in *Pseudotsuga* forests (40%), *Abies* forests, and alpine tundra (50%+). Recent studies (e.g. Munn 1977) describe stonier grassland soils because most relatively stone-free grasslands have been converted to agricultural use.

Percentages of clay in the soil decrease as percentages of coarse material increase; they are about 30% in grasslands and *Pinus* forests and 10% in higher forest and tundra sites (Table 1). The different particle size distributions are probably due to the facts that 1) clays are more readily transported away from mountain tops than are stones or sands, 2) clays may form more rapidly under warmer conditions found under grasslands than under cooler forests above them, and 3) shales are more important at lower elevations.

Percentages of organic carbon in surface soils rise as one moves from light colored soils of *Bouteloua* grasslands (1.5%) to darker soils of *Festuca* grasslands (4%), to peaty tundra sites dominated by graminoids (7%) (Table 1). The upward trend in soil organic carbon concentrations observed under graminoid vegetation is interrupted under forest lands with soils of lighter colors and lower organic carbon contents; *Pinus* (2%), *Pseudotsuga* (1%), and *Abies* (1%). Soil organic matter is reported to rise continually with altitude in the southwest United States (Whittaker *et al.* 1968, Hannawalt and Whittaker 1976); the difference in our observations could be due to the presence of grassy rather than shrubby understories in their forests or to the inclusion of an organic (O) horizon in their soil samples.

The capacity of the soil to retain water decreases as one moves from dry grasslands to high forests (Table 1). In the A-horizon, for example, water held at a tension of 15 bars was about 11% (wt/wt) for most grasslands (cf *Festuca scabrella* 15%), it declined to 5% or less in conifer forests, and then rose to 9% in alpine tundra. The high water holding

TABLE 1. PHYSICAL CHARACTERISTICS OF SOILS ASSOCIATED WITH SEVEN ROCKY MOUNTAIN VEGETATION SERIES.

Series <sup>1</sup>	Hor <sup>2</sup>	Thick, dm <sup>2</sup> X ± SE <sup>6</sup>	Stone % <sup>3</sup> X ± SE	Sand % <sup>3</sup> X ± SE	Clay % <sup>3</sup> X ± SE	OC % <sup>4</sup> X ± SE	WP % <sup>5</sup> X ± SE
<i>Alpine tundra</i>	Dm	1.0	50	56	10	5.7	8.0
	A	2.0	50	55	9	6.8	9.0
	B	2.5	60	55	11	2.2	11.3
<i>Abies lasiocarpa</i>	Dm	1.0	15	52	4	1.6	5.4
	A	5.3	33	62	3	0.6	2.7
	B	16.0	64	70	4	0.0	1.6
<i>Pseudotsuga menziesii</i>	Dm	1.0±0.0	13± 9	36± 5	12± 2	1.2±0.2	6.4±1.1
	A	5.5±1.3	21±11	45± 8	12± 2	0.5±0.7	5.0±0.7
	B	7.6±1.1	32±14	36± 7	24± 3	0.2±0.1	8.6±1.2
<i>Pinus ponderosa</i>	Dm	1.0±0.0	0± 0	36±14	28± 8	2.9±0.5	11.7±1.7
	A	1.9±0.2	0± 0	19± 6	28± 8	2.0±0.5	11.8±1.4
	B	7.0±1.6	2± 2	28±10	37±10	0.5±0.1	12.2±2.0
<i>Festuca scabrella</i>	Dm	1.0±0.0	2± 1	24± 6	30± 2	5.6±1.5	16.8±2.2
	A	2.9±0.5	4± 2	26± 6	29± 2	4.2±1.2	14.7±1.8
	B	8.9±0.7	12± 4	28± 9	38± 4	0.4±0.2	12.5±0.6
<i>Festuca idahoensis</i>	Dm	1.0±0.0	7± 5	36± 4	27± 3	2.8±0.7	11.3±1.0
	A	1.4±0.2	7± 5	39± 3	23± 3	3.9±0.7	11.1±1.0
	B	4.0±0.5	3± 2	29± 6	31± 2	1.2±0.1	12.8±0.9
<i>Agropyron spicatum</i>	Dm	1.0±0.0	0± 0	45± 9	23± 1	3.1±0.5	13.9±1.2
	A	1.2±0.4	0± 0	47± 8	23± 1	2.9±0.4	13.0±0.1
	B	3.5±0.4	0± 0	41±12	32± 4	1.0±0.1	14.0±1.0
<i>Bouteloua gracilis</i>	Dm	1.0±0.0	0± 0	33± 3	28± 2	1.5±0.1	11.4±0.6
	A	1.6±0.2	0± 0	33± 3	27± 2	1.5±0.1	11.2±0.6
	B	4.1±0.4	0± 0	29± 4	34± 2	0.8±0.1	12.9±0.7

- 1) Numbers following vegetation types indicate numbers of series considered and numbers of benchmark soils studied.
- 2) Horizons are the 0-10 cm layer (Dm), the A horizon, and the B horizon. Their average thickness are given in decimeters.
- 3) Stone % is the percentage of the horizon filled with stones 2 mm or more in diameter. Sand %, silt % and clay % make up 100% of the remaining soil volume.
- 4) Organic carbon (OC) is a % of total fine soil weight. Multiply by 1.7 for organic matter.
- 5) 'Wilting percentage' is the water content of the soil held at tensions of 15 bars expressed on a weight-weight basis.
- 6) Mean and standard error, N is given by the second number under each vegetation type.

capacity of dry grassland soils is due to their high clay contents; the increase in water holding capacity seen in moister grasslands is likely due to increasing organic matter contents; the low water holding capacities of forest soils are due to decreases in both organic matter and clay contents; and the high water holding capacities of alpine tundra soils must be due almost completely to their high organic matter contents since their clay contents are low. In southern California where both clay and organic matter contents are reported to increase with altitude water holding capacities increase from desert shrublands to high forests (Hannawalt and Whittaker 1976).

Nitrogen concentrations (Kjeldahl) in the soil rise as one approaches the forest margin, fall as one moves up the altitudinal gradient through conifer forests, and continue their original rise in the alpine (Table 2). This trend parallels that of organic matter content since most of the nitrogen is organic nitrogen.

Carbon/nitrogen ratios (calculable from Tables 1 and 2) rise as one moves from low grasslands to high forests. In the A-horizon, for example, they are 10, 11, 12, 12, 15, 17, 20, and 15 for *Bouteloua*, *Agropyron*, *Festuca*, *Festuca*, *Pinus*, *Pseudotsuga*, *Abies* and tundra soils. Such a trend would appear either if organic matter were in a more advanced stage of decay at lower altitudes (due to warmer temperatures) and/or if organic matter of the forested zones were initially poorer in nitrogen than that of grasslands. The latter possibility is not true for leaves alone but it appears to be true when one includes carbon rich woody material (cf Rodin and Bazelevich 1965). Whittaker *et al.* (1968) also observed that C/N ratios rose from 5 to 30 with increasing altitude.

Data on phosphorus availability in the benchmark soils was too sparse to analyze. Data of Spillsbury and Tisdale (1944) show a decline in available phosphorus up our vegetational gradient (813 to 34 ppm in the A-horizon, method not reported). Other data (Munn 1977 and Nimlos and McConnell 1965) show no clear trend in phosphorus availability from *Bouteloua* to *Festuca* to alpine tundra vegetation (average 18 ppm in the A-horizon, Bray phosphorus) and less phosphorus in the B than in the A-horizon. The second data set appears to be more generally applicable.

The capacity of the soil to retain nutrients parallels its capacity to hold water since both are determined by clay and organic matter contents. Anion exchange capacity, a measure of the capacity of a soil to retain negatively charged ions ( $\text{NO}_3^-$  and  $\text{SO}_4^{2-}$ ) is low in our soils and is rarely measured. Cation exchange capacity (meq/100 gms) rises from dry grasslands (20) to *Festuca scabrella* grasslands (25), declines through the conifer forests (20 to 4), and rises again in the alpine (11). Data from a vegetation gradient in southern California (Hannawalt and Whittaker 1976) show a parallel peak of cation exchange capacity (both natural and organic matter free) just below pine forests.

The pH in the A-horizon declined from 7.4 in *Bouteloua* grasslands to 7 in *Agropyron* grasslands, 6.3 in *Festuca* grasslands, and 5.5 in higher conifer forests and tundra. Similar pH declines are recorded by Daubenmire

TABLE 2. CHEMICAL CHARACTERISTICS OF SOILS ASSOCIATED WITH SEVEN ROCKY MOUNTAIN VEGETATION TYPES.

Vegetation <sup>1</sup>	Hor <sup>2</sup>	N % <sup>3</sup>		Ca <sup>4</sup>		Mg <sup>4</sup>		CEC <sup>4</sup>		pH <sup>5</sup>	
		X ± SE <sup>6</sup>	X ± SE	X ± SE	X ± SE	X ± SE	X ± SE	X ± SE	X ± SE		
<i>Alpine tundra</i>	Dm	0.50	0.3	6.7	1.6	9.0	5.4				
	A	0.45	0.3	7.1	2.4	10.5	5.6				
1-1	B	0.20	0.2	2.3	0.8	4.3	5.6				
<i>Abies lasiocarpa</i>	Dm	0.07	0.5	1.8	0.6	7.9	6.1				
	A	0.03	0.2	0.9	0.4	3.7	5.7				
1-1	B	0.01	0.1	0.7	0.6	2.5	5.2				
<i>Pseudotsuga menziesii</i>	Dm	0.07±0.00	0.5±0.1	5.4±0.8	1.7±0.3	9.6±1.6	5.6±0.3				
	A	0.03±0.01	0.3±0.1	4.0±0.1	1.5±0.3	7.0±0.9	5.6±0.2				
3-5	B	0.02±0.01	0.3±0.1	8.3±1.7	4.0±0.7	12.1±2.0	5.9±0.2				
<i>Pinus ponderosa</i>	Dm	0.19±0.03	1.0±0.3	14.8±2.5	3.3±0.8	24.2±2.8	6.4±0.3				
	A	0.13±0.03	0.8±0.2	13.8±1.9	3.9±0.9	20.7±2.3	6.4±0.3				
5-8	B	0.04±0.01	0.3±0.1	13.0±1.6	4.2±1.2	19.4±2.1	6.5±0.2				
<i>Festuca scabrella</i>	Dm	0.47±0.10	1.9±0.3	21.2±3.1	4.1±0.8	30.7±3.6	6.2±0.1				
	A	0.36±0.08	1.6±0.2	17.2±2.6	3.7±0.6	26.4±3.5	6.2±0.2				
2-4	B	0.07±0.02	0.5±0.1	13.4±2.3	4.8±1.0	20.2±3.6	6.8±0.2				
<i>Festuca idahoensis</i>	Dm	0.30±0.02	1.0±0.2	14.0±1.8	3.4±0.5	22.0±2.1	6.5±0.1				
	A	0.31±0.06	1.0±0.2	13.7±1.7	3.4±0.5	22.0±2.3	6.5±0.1				
6-11	B	0.09±0.02	0.6±0.0	17.4±2.8	5.8±1.0	26.2±2.9	7.1±0.2				
<i>Agropyron spicatum</i>	Dm	0.28±0.05	1.7±0.4	17.9±1.8	3.1±0.3	23.5±1.7	6.8±0.2				
	A	0.26±0.04	1.7±0.5	16.8±1.0	3.1±0.1	22.4±0.8	6.9±0.3				
2-4	B	0.10±0.02	1.0±0.3	24.6±2.4	4.5±0.1	26.4±1.6	7.1±0.4				
<i>Bouteloua gracilis</i>	Dm	0.15±0.02	1.2±0.0	14.6±0.7	5.2±0.5	20.2±1.0	7.4±0.2				
	A	0.15±0.02	1.2±0.1	14.5±0.6	5.3±0.5	20.1±1.0	7.4±0.2				
3-15	B	0.09±0.01	0.7±0.0	16.5±2.8	7.0±1.6	21.7±1.0	8.1±0.1				

- 1) Numbers following vegetation types indicate numbers of series considered and numbers of benchmark soils studied.
- 2) Horizons are 0-10 cm (Dm), A, and B. Their physical characteristics are described in Table 1.
- 3) Nitrogen is expressed as a % of fine soil weight.
- 4) Potassium, calcium, magnesium, and cation exchange capacity (CEC) are expressed in millequivalents per 100 grams. % base saturation, calculated as quantity of (K + Ca + Mg)/CEC, for A horizons of our soils are alpine tundra 46%, *A. lasiocarpa* 41%, *P. menziesii* 83%, *P. ponderosa* 89%, *F. scabrella* 85%, *F. idahoensis* 82%, *A. spicatum* 96% and *B. gracilis* 100%.
- 5) pH was generally measured on a 1 soil : 1 water paste.
- 6) Mean and standard error; N is given by the second number under each vegetation type.

and Daubenmire 1968, Whittaker *et al.* 1968 and Hannawalt and Whittaker 1976).

The fact that pH declines as one moves up the vegetation gradient suggests that the base saturation must decline. If one expresses the sum of potassium, calcium, and magnesium concentrations (meq/100 gm) as a percent of cation exchange capacity for the A-horizon he obtains base saturations of 100, 96, 82, 85, 89, 83, 41, and 93% for *Bouteloua*, *Agropyron*, *Festuca*, *Festuca*, *Pinus*, *Pseudotsuga*, *Abies* and alpine tundra respectively. The reader will observe (Table 2) that concentrations of potassium, calcium, and magnesium are all relatively high in grasslands, that they decline through conifer forests, and that they rise in the alpine tundra. The low pH and low base availability of higher stands may be due to the relatively high precipitation levels on these sites.

Soil water holding capacity. Soils serve plants as a nutrient pool, as a buffer against drought, and as a source of support. Their success as buffers against drought depends on their water storage capacities and on the distribution of buffer filling precipitation.

The water storage capacity (cm of rain) of a soil is calculated by multiplying (1 cm<sup>2</sup> of surface x soil depth (cm)) x (100-percent stone) x (bulk density (gm/cc)) x (water holding capacity at 1/3 bar (%)) - water holding capacity at 15 bars (%)). It is clear therefore 1) that increasing soil depth with altitude increases water holding capacity, 2) that increasing stone content with altitude decreases water holding capacity, and 3) that decreasing soil water holding capacities of the fine earth fraction of the soil with altitude (except *Festuca scabrella*) decreases water holding capacity. Bulk densities of soils averaged 1.30 ± 0.06 gm/cc for the A-horizon of grassland soils, 1.59 ± 0.05 gm/cc for the A-horizon of forest soils, and 1.70 ± gm/cc for the B-horizon of both forest soils and grassland soils. If these bulk density estimates were high, water holding capacities would be overestimated in proportion to the error.

Water holding capacities were calculated for three layers in each type (Table 3); all showed increasing water holding capacity as one moves from *Bouteloua* to *Festuca* grasslands and decreasing water holding capacities as one progresses upward to alpine tundra sites. 1) The A horizon was considered because as 'the horizon of organic matter accumulation' it presumably represents the zone of maximum root activity and a minimum estimator of the layer exploited by plants. Its water holding capacity declines both upward and downward from the grassland-forest boundary; *Bouteloua gracilis* grasslands 2.5 cm, *Festuca scabrella* grasslands 5.2 cm, and alpine tundra 0.9 cm. 2) The whole solum was considered because roots and organic matter, though dilute, are usually found throughout it and in significantly greater quantities than in the C-horizon below. The water holding capacity of the solum also declines as one leaves the grassland-forest boundary; *Bouteloua gracilis* 12 cm, *Festuca scabrella* 22 cm, and alpine tundra 3.8 cm. 3) In the comparisons made above the thicknesses of soil layers considered varied between vegetation types. Since root concentrations generally decline sharply (logarithmically) with depth (Brady 1974) one may want to compare water holding capacities of a layer of constant thickness beneath different

TABLE 3. AVAILABLE WATER HOLDING CAPACITY, TOTAL CARBON AND NITROGEN CONTENTS, AND CONTENTS OF AVAILABLE POTASSIUM, CALCIUM, AND MAGNESIUM IN SOILS ASSOCIATED WITH SEVEN ROCKY MOUNTAIN VEGETATION SERIES.

Vegetation <sup>1</sup>	Hor <sup>2</sup>	Thick (dm) X ± SE <sup>5</sup>	Water (cm) <sup>3</sup> X ± SE	OC t/ha <sup>4</sup> X ± SE	N t/ha <sup>4</sup> X ± SE	K t/ha <sup>4</sup> X ± SE	Ca t/ha <sup>4</sup> X ± SE	Mg t/ha <sup>4</sup> X ± SE
Alpine tundra	A	1.0	0.9	68.0	4.5	0.1	1.4	0.3
	0-5	5.0	4.4	135.0	10.6	0.3	2.8	0.6
1-1	A+B	4.5	3.8	124.0	9.6	0.3	2.6	0.5
	A	5.3	1.5	32.5	1.7	0.4	1.0	0.3
<i>Abies lasiocarpa</i>	0-5	5.0	1.4	30.5	1.6	0.4	0.9	0.3
	A+B	21.5	3.0	35.5	2.6	0.8	2.4	1.0
<i>Pseudotsuga menziesii</i>	A	5.5±0.7	3.1±0.6	29.0± 4.3	1.7±0.4	0.9±0.2	5.7± 0.9	1.3±0.2
	0-5	5.0±0.0	3.6±0.7	28.4± 5.4	2.4±0.4	1.0±0.2	6.9± 0.7	1.7±0.2
3-5	A+B	13.3±1.3	10.3±1.6	45.0± 6.5	3.6±0.4	2.0±0.3	15.3± 3.0	4.9±0.8
	A	1.9±0.2	3.7±0.7	59.0±18.1	3.8±1.0	0.9±0.3	8.7± 1.8	1.4±0.3
<i>Pinus ponderosa</i>	0-5	5.0±0.0	9.5±1.4	83.1±18.0	5.7±1.1	1.9±0.6	20.1± 3.0	4.3±0.9
	A+B	8.8±1.5	16.8±4.4	113.5±23.6	8.6±1.7	2.5±0.7	38.8± 8.4	8.9±2.6
<i>Festuca scabrella</i>	A	2.9±0.6	5.2±0.8	141.3±31.2	10.8±2.5	2.3±0.6	12.6± 2.2	1.5±0.2
	0-5	5.0±0.0	9.0±0.7	153.5±36.7	13.3±2.9	2.9±0.5	21.4± 2.6	3.5±0.6
2-4	A+B	11.8±0.4	21.8±0.6	188.0±47.3	21.1±5.0	5.2±0.9	56.8±10.0	10.1±2.3
	A	1.3±0.2	2.0±0.4	53.0±14.3	4.3±0.9	0.6±0.2	4.6± 0.8	0.8±0.3
<i>Festuca idahoensis</i>	0-5	5.0±0.0	9.2±0.8	120.6±21.5	9.9±1.6	1.7±0.2	24.9± 3.5	4.4±0.6
	A+B	5.3±0.5	10.1±1.8	130.6±30.0	11.0±2.3	1.9±0.4	27.2± 2.6	6.1±1.4
<i>Agropyron spicatum</i>	A	1.2±0.3	2.4±1.1	46.7±17.1	4.2±1.5	1.0±0.2	6.3± 3.2	0.7±0.4
	0-5	5.0±0.0	10.8±0.3	110.4±10.6	10.9±1.0	3.6±0.9	37.0± 5.0	4.0±0.1
2-4	A+B	4.8±0.4	11.7±1.5	108.3±19.8	8.5±2.9	3.7±0.7	39.2± 1.1	4.2±0.3
	A	1.6±0.2	2.5±0.3	29.7± 2.4	2.8±0.2	1.0±0.1	5.7± 0.9	1.4±0.3
<i>Bouteloua gracilis</i>	0-5	5.0±0.0	9.6±0.5	74.3±21.3	7.9±0.7	2.4±0.2	28.4± 3.0	4.7±1.0
	A+B	5.8±0.6	11.7±1.2	82.0± 7.5	8.6±0.6	2.7±0.3	32.6± 3.2	7.1±2.2

1) Numbers following series names indicate the number of soil series representing the vegetation series and the total number of benchmark soils representing the vegetation series.  
 2) Horizons considered are the A, A+B (solum), and the 0-5 dm layer.  
 3) Water holding capacity of the soil layer considered was calculated as volume x % fine soil x bulk density x (1/3 bar water - 15 bar water).  
 4) Quantities of total nitrogen, total organic matter carbon, and available nutrients in soil layers were calculated as volume x % fine soil x bulk density x nutrient concentration. Organic carbon may be converted approximately to organic matter by multiplying OC x 1.7.  
 5) Mean and standard error, N is given by the second number under each vegetation type.

vegetation types. A thickness of 50 cm was selected because root sampling data suggest that 75% of the roots of all vegetation types considered are likely to be in the 0-50 cm layer (Weaver 1977). The water holding capacity of the 0-50 cm layer is essentially constant from dry grasslands to low forests and declines sharply in higher forests: *Bouteloua gracilis* 9.6 cm, *Pinus ponderosa* 9.5 cm, and *Abies lasiocarpa* 1.4 cm.

Seasonal soil water availability. Seasonal availability of water at a site depends not only on the size of its soil water reservoir but also on the flows into it (precipitation, capillary rise or lateral percolation) and flows out of it (vertical percolation, lateral percolation or evapotranspiration). It may be measured by 1) subtracting overflows and outflows from inflows (bookkeeping method) or 2) by measuring the amounts of water in the reservoir periodically (dipstick method). In 1972-1973, a dry year, water was scarce (i.e., stresses were greater than -10 bars) in the top 75 cm of the soil for 3-5 months in *Agropyron-Bouteloua* stands, for 1-2 months in *Festuca idahoensis* stands, for 0-2 months in *Pseudotsuga* stands, and no months in *Abies lasiocarpa* stands (Weaver 1977) in spite of the smaller capacities of the storage reservoirs of forest stands. Data from similar stands west of the Rocky Mountains (Daubenmire 1969) also show that water stress periods in forest vegetation types are shorter than those experienced by grassland vegetation types. Since the water storage capacities of our forest soils are so small, inputs must be more frequent and/or outflows must be considerably smaller than those experienced by grasslands to provide the relatively short drought periods observed.

Nutrient pool sizes. Estimated nutrient pool sizes should integrate the various soil nutrient supplying factors presented above, just as total soil water holding capacity provided a 'plants eye view' of soil water. The pool size can be estimated by multiplying surface area (cm<sup>2</sup>) x soil depth (cm) x (100-percent stone) x available nutrient concentrations (gm/100 gm). It is clear therefore 1) that increasing soil depth with increasing altitude increases nutrient pool sizes, 2) that increasing stone content with altitude decreases pool sizes, and 3) that the tendency of carbon, nitrogen, potassium, calcium, and magnesium concentrations to decline with altitude (or to peak under *Festuca* grasslands) results in declining nutrient pool sizes. It will be obvious that calculations for layers (eg A- and B-horizons) with different characteristics had to be made separately and summed. Three soil horizons were considered: The A-horizon (because the greatest biological activity occurs here), the solum (= sum of A- and B-horizons, because most biological activity occurs here), and the 0-50 cm layer (because this is a layer of uniform thickness in which much of the biological activity occurs).

Quantities of organic matter stored in grassland soils increased with increasing altitude. Organic carbon in the A- and B-horizons rose from *Bouteloua* (82 T/ha) to *Agropyron* (108 T/ha) to *Festuca* (130-190 T/ha) to alpine tundra (124 T/ha). In the forest zone it fell from *Pinus* (113 T/ha) to *Pseudotsuga* (45 T/ha) to *Abies* (35 T/ha). Despite the large quantities of carbon stored as tree trunks and litter aboveground total carbon stored in forest ecosystems probably does not significantly exceed that of the moister grasslands: standing crops of mature forests (1.2 x aboveground

biomass x 0.4 gm carbon/gm organic matter) in the northern Rocky Mountains are approximately 40-80 T/ha under *Pinus*, 80-160 T/ha under *Pseudotsuga*, and 90 T/ha under *Abies* (Weaver and Forcella 1978).

Kjeldahl nitrogen in the A- and B-horizons rose from 9 T/ha under *Bouteloua* to 21 T/ha under *Festuca*, fell to 2 T/ha under *Abies* and rose to 9.6 T/ha under alpine tundra (Table 3). Like carbon, nitrogen stored in tree trunks is insufficient to eliminate the dip which occurs under forests in the curve of nitrogen storage plotted against altitude (Weaver and Forcella 1978).

Quantities of easily available (ammonium acetate extractable) potassium, calcium, and magnesium in the solum are highest under *Festuca scabrella*, lower under drier grasslands and considerably lower under high forests and alpine tundra (Table 3). It will be argued below that the quantity of potassium required by each ecosystem is greater than that present in the A-horizon, but less than that in the A- and B-horizons while the A-horizons contain an excess of calcium and magnesium except in the alpine. Of potassium, A-horizons contain 0.5 to 1 T/ha except under *Festuca scabrella* (2.3 T/ha), *Abies* (0.4 T/ha), and alpine (0.1 T/ha). Of calcium, A-horizons contain 6 T/ha under *Bouteloua*, 12 T/ha under *Festuca scabrella*, 1 T/ha under *Abies*, and 1.4 T/ha under alpine tundra. Of magnesium, the A-horizons contain 0.7 to 1.5 T/ha under grasslands and low forests and 0.3 T/ha under *Abies* forests and alpine tundra.

Total harvest (including leaves and branches) of forests may remove significant quantities of the easily available nutrients (i.e., those extractable from soils with ammonium acetate and those bound in plant material). For example, if a *Pseudotsuga* stand contains 180 T/ha of organic matter and if nutrients bound in that vegetation are 0.16-0.46 T nitrogen/100 tons of organic matter, 0.08-0.18 T potassium/100 T OM, and 0.12-0.50 T calcium/100 T OM then total harvest of that stand would remove 11-19% of the nitrogen, 7-14% of the potassium, and 1-6% of the calcium. Biomasses of other mature forests of the northern Rocky Mountains are likely to range from 0.7 to 3.4 hundreds of tons of organic matter per hectare (Weaver and Forcella 1977).

Horizonation and limiting factors. The ratio of mineral concentrations in the A-horizon to those in the B-horizon may be taken as an index of horizonation. It is argued below that nutrient elements which are more concentrated in the A- than in the B-horizon are near limiting and that this index can serve as a tool for recognizing possibly limiting nutrients.

If a mineral is less concentrated in the A-horizon than in the B-horizon we can conclude that it is being (or has been) leached out of the A-horizon. For example, clay concentrations in the A-horizon are about 90% of those in the B-horizon throughout our vegetational gradient (Table 1). Sodium concentrations in the Colorado alpine are markedly lower in the A-horizon than in the B-horizon (Retzer 1956).

If a relatively soluble mineral is more concentrated in the A-horizon than in the B-horizon we can conclude 1) that in the absence of biological nutrient pumping the mineral would be leached downward from both the A- and B-horizons, 2) that the nutrient is being pumped from the B- to the A-horizons at rates equaling or exceeding the rates of downward leaching, 3) that the nutrient is bound in the A-horizon in a biologically related form, i.e., covalently in organic matter or via continued upward transport and 4) that--to the extent that production exceeds decomposition in the ecosystem--the system is dependent on import of that nutrient from the B-horizon, i.e., production in the system will be limited by the turnover rate of that element when the B-horizon is exhausted. Phosphorus concentrations are approximately twice as great in the A-horizon of our grasslands and tundra ecosystems as in the B-horizons (Munn 1977, Nimlos and McConnell 1965). Potassium concentrations (Table 2) are approximately twice as great in the A-horizon as in the B-horizon in most vegetation types, except *Pinus* (2.7 x) and *Festuca scabrella* (3.2 x). Calcium and magnesium concentrations are higher in the A-horizon than in the B-horizon of alpine tundra (3.2).

If a relatively soluble essential element is more concentrated in the B-horizon than in the A-horizon we can conclude 1) that leaching from the A-horizon exceeds (or has exceeded) biological pumping into it, 2) that the quantity of the nutrient in the A-horizon is equal to or greater than that required by the biological components of the ecosystem occupying the site and 3) that in sufficient time (i.e., after sufficient leaching) the concentrations of these elements in the A-horizon will exceed those in the B-horizon. Quantities of magnesium in the A-horizon may, then, be limiting in alpine communities but not in the other communities studied. Quantities of calcium are certainly not limiting in dry grasslands though they may be limiting in moister vegetation types--especially in alpine tundra.

A relatively immobile mineral (e.g. silica) should be concentrated in the A-horizon than in the B-horizon because soluble materials in the soil will be leached into lower layers thereby increasing the representation of the immobile mineral in the A-horizon and decreasing the representation of immobile mineral in the B-horizon by dilution of it.

Concentrations of nutrient cations may be expressed either as grams/gm of soil (equivalent to the meq/100 gm of soil of Table 2) or as a percentage of the soil's cation exchange capacity. The conclusions drawn above hold in either case. The conclusion that calcium may be limiting in *Festuca scabrella* and possibly in *Pinus* and *Abies* ecosystems is supported by the first but not by the second expression.

Organic matter is usually about three times as concentrated in the A-horizon as in the B-horizon because it is injected into the surface soils. Soil organic carbon ratios lie between 2.5 and 4.5 in all ecosystems except *Bouteloua* (1.9), and *Festuca scabrella* (11). Soil nitrogen (Kjeldahl) ratios lie between 2.2 and 3.4 in all ecosystems but *Bouteloua* (1.7) and *Festuca scabrella* (5.1).

One may speculate that the production of every mature ecosystem is limited by one or more mineral elements more concentrated in the A- than in the B-horizon. 1) Early in succession the production of most ecosystems is limited by elements with gaseous cycles: carbon and oxygen (CO<sub>2</sub>) due to stomate closure (lack of water) or nitrogen due to low fixation rates. We assume that energy and water supplies are specified in the ecosystem definition and that they do not change during succession; if not, they should be listed with carbon, oxygen, and nitrogen. 2) As succession proceeds organic matter accumulates with concurrent binding of other nutrient elements and leaching of all unbound nutrient elements downward. 3) In time, one of the mineral elements will disappear from the B-horizon due to nutrient pumping upward and leaching downward and it will become limiting. That element will not be carbon, oxygen, hydrogen, or nitrogen since additional supplies of these elements will be available from the atmosphere (cf Likens *et al.* 1978). 4) Since organisms have a fixed elemental composition the quantities of the remaining mineral elements the system can bind will be determined and all excesses will slowly be leached out. When they are, all mineral elements will be equally limiting and there will be no 'fertilizer response' if only one of the limiting elements is applied. 5) The richness of the mature ecosystem occupying a site will depend, then, on the initial supply of the limiting nutrient and the amount of that element bound in biologically related forms before all of the remaining material is leached out of the system. 6) The reader will have noted that this argument depends on a steady state system in which inputs (e.g. fertilizer) and losses (e.g. erosion) are small relative to the rates of soil forming processes.

With respect to Montana ecosystems we can conclude 1) that none of the ecosystems is fully mature in the sense that all essential nutrients are absent from the B-horizon, 2) that all of the ecosystems are approaching maturity because in each at least one element (potassium and likely phosphorus) is more concentrated in the A- than in the B-horizon and 3) that the most mature systems are alpine ecosystems where several elements are more concentrated in the A- than in the B-horizon.

Causes of changes in pool sizes along an altitudinal gradient. During succession at any site organic matter will accumulate to an equilibrium level. 1) Early in succession production exceeds decomposition, perhaps because photosynthetic rates occurring in sunwarmed leaves exceed respiratory processes in cool soils. The presence of organic matter is essentially all soils supports this statement. 2) The rate of organic matter increase is determined by factors determining production (e.g. temperature, water and nutrient availability) and decomposition (e.g. temperature and oxygen availability). 3) The fact that an equilibrium is reached--that organic matter does not accumulate indefinitely--implies that net production must decrease as the quantity of organic matter present increases. Gross production might be slowed to equal decomposition (including respiration) if supplies of an essential element were converted to organic forms available only through decomposition or, less likely, if appropriate amounts of autotoxic substances were produced. One can also imagine mechanisms by which decomposition rates could increase to equal production rates: the probability of fire (or harvest) increases as organic matter accumulates, respiration rates rise

relative to photosynthetic rates as plants mature, efficiencies of individual consumers may rise as organic matter accumulates and/or efficiencies (gm/m<sup>2</sup>/yr) of a consumer population might rise if the efficiencies of individuals remained constant while their numbers increased with increases in the amount of decomposing material. 4) When the organic matter equilibrium is reached excesses of essential nutrients will be leached away until the system is also limited by them.

The equilibrium organic matter level is characteristic of the ecosystem observed. As noted above, organic carbon in the soil (and in the ecosystem) increases from 80 to 180 T/ha as one moves from low to high grasslands. Organic carbon in the soil shows the opposite trend under forests (114 to 35 T/ha) though inclusion of the remaining carbon in the ecosystem (Frees and litter) could conceivably continue the trend. If we assume the latter, we empirically expect the trend because higher sites are both cooler and moister (Jenny 1941); and since we have little reason to believe that cool moist sites are especially well endowed with nutrients or toxin producing plants we might tentatively conclude that this empirical trend is due to a decreasing ability of decomposers to efficiently consume dilute organic matter in cool moist sites where, for example, fires might be uncommon and small soil oxygen supplies might inhibit bacteria and fungi. If, on the other hand, we assume that both soil and ecosystem carbon levels are lower in ecosystems both upslope and downslope from *Festuca scabrella* grasslands, we might conclude that density dependent decomposition regulates organic matter levels in the lower part of the transect and that nutrient limited production regulates organic matter levels in the upper part of the transect where quantities of nutrients available in the solum become smaller and smaller.

The equilibrium level of other biological materials parallels that of carbon. Nitrogen and calcium contents of the A- and B-horizons rise to the forest border, fall through the forests, and rise slightly in alpine tundra. Potassium and magnesium rise to the forest border and fall to alpine tundra. This relationship arises because these elements are bound to organic matter or are pumped at rates proportional to root biomasses present. The failure of potassium and magnesium to rise with nitrogen and calcium as one moves from the forest to tundra sites may be attributed to their relatively loose binding to organic materials.

Change in pool size with season. Quantities of nutrients available in the soil might be expected to vary with season as they are bound by growing organisms and released by microbes. Available nutrients in soils under *Festuca idahoensis*, *Artemisia tridentata*, *Populus tremuloides*, and *Pseudotsuga menziesii* vegetation are lowest at mid-winter (January through April) and peak in early fall (September and October); average minimal values as a percent of maximal values in 1974 were nitrate 27%, ammonium 30%, phosphorus 45%, sodium 60%, potassium 65%, calcium 77%, magnesium 82%, and organic matter 80%. Seasonal variation in nutrient availability was slight in soils under an *Abies lasiocarpa* forest (Weaver and Forcella 1979).

## CONCLUSIONS

Soils associated with major vegetation types along an altitudinal gradient are described. From dry to wet the vegetation series considered are *Bouteloua gracilis*, *Agropyron spicatum*, *Festuca idahoensis*, *Festuca scabrella*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, and alpine tundra.

Water storage capacities in the solum rise from 12 cm under *Bouteloua gracilis* to 22 cm under *Festuca scabrella* and fall to 3 cm under alpine tundra. Despite this, water stress periods fall from 5 to 3 months in *Bouteloua gracilis* and *Agropyron spicatum* grasslands to 1 to 2 months in *Festuca* grasslands to zero months in high forests.

Quantities of soil organic carbon in ecosystems increase from *Bouteloua gracilis* to *Festuca* ecosystems, decline through conifer forests and rise again in the alpine.

Pool sizes of other nutrient elements are usually correlated with quantities of soil organic carbon either because they are covalently bound to it (N and Ca) or because they are pumped at rates proportional to root biomass (K and Mg). The failure of potassium and magnesium quantities to rise, as nitrogen and calcium do, with the rise in organic carbon when one moves from the conifer forests to alpine tundra is attributed to the relatively high susceptibility of potassium and magnesium to leaching.

It is suggested that a near-limiting nutrient element can be recognized by its greater concentration in the A-horizon than in the B-horizon. If so, potassium is near limiting throughout the gradient, and calcium and magnesium are near limiting in alpine ecosystems. Though data are inadequate to draw this conclusion they suggest that phosphorus may also be near limiting throughout the gradient.

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