Great Basin Naturalist 58(4), © 1998, pp. 352–362

SOIL-VEGETATION RELATIONS OF RECOVERING SUBALPINE RANGE OF THE WASATCH PLATEAU

James O. Klemmedson[1] and Arthur R. Tiedemann[2]

ABSTRACT.—On degraded subalpine range of the Wasatch Plateau, we examined the hypothesis that recovery of vegetation, as manifested by its composition and biomass yield, was related to soil phosphorus (P) and sulfur (S) status. We sampled 6 topographic locations to determine the relationship among composition and yield of grasses and forbs, litter cover, and soil characteristics including rock cover, organic carbon (C_0), total N (N_t), available nitrogen (N_{av}), total phosphorus (P_t), organic P (P_0), inorganic P (P_i), total potassium (K), total S (S_t), and element ratios. We also evaluated aspect effects. An alternative hypothesis was that productive potential was a function of depth of soil remaining after the period of destructive grazing. Differences among locations were significant for all vegetal attributes and for all soil characteristics except total K and C_0. Aspect was significant only for forb yield and P_t. Regression coefficients for yield and percentage composition of grasses were always opposite in sign to those for forbs. Yield and composition of grasses and forbs as groups were oppositely and strongly related to soil element ratios of C_0/P_t, N_t/P_0, C_0/P_t, and C_0/S_t but were not related to soil P_t or S_t. There was no clear support for acceptance of the hypothesis that soil P and/or S were major factors in recovery of this subalpine range after destructive grazing. Differences in regression coefficients and lower r-values among species within grass and forb groups, than for the groups themselves, to soil variables is a reflection of species individuality. This indicated a need to examine soil/vegetation relationships at the species level. Percentage compositions of grasses and forbs were oppositely related to the depth of A + B horizon, lending support to acceptance of the alternative hypothesis.

Key words: summer range, plant composition and cover, herbage yield, litter, soil C, N, P, S, and K.

After 35 years of destructive grazing by cattle and sheep in the late 1800s, the subalpine range of the Wasatch Plateau east of Ephraim, Utah, was in poor condition (Reynolds 1911, Sampson and Weyl 1918, Sampson 1919). Depletion of vegetation reached such severe proportions that most of the soil A horizon was lost by erosion and mud-rock floods were a common occurrence in the canyons and valleys below (Reynolds 1911, Croft 1967). In many places only subsoils remained when grazing regulation was begun with the 1903 establishment of the Manti National Forest (Reynolds 1911, Sampson and Weyl 1918, Ellison 1949). Transient livestock herds were abolished and livestock numbers greatly reduced, but most of the summer range was so badly deteriorated that these management changes were insufficient to halt continuing soil loss (Ellison 1954). Although condition of the range improved over the next 4 decades, most of the summer range was still unstable in 1950 and accelerated erosion was continuing, but at much reduced rates (Ellison 1954, Meeuwig 1960).

Our observations suggest that improvement in soil and vegetal conditions reached a plateau about 1930–1940, based on Ellison's (1954) records, and has remained essentially the same from the time of Ellison's studies (Intermountain Research Station, Provo, Utah, unpublished data; Johnson 1964). These observations led us to ask why, after 30–40 yr of rapid improvement under reduced grazing pressure, should secondary succession apparently stabilize at a midseral stage and remain so until the present?

There are perhaps several possible explanations for the apparent stable state (Lewontin 1969, Laycock 1991) that exists on the Wasatch summer range. Two explanations derive chiefly from degradation of the ecosystem and massive erosion that occurred over the long period of livestock overgrazing: (1) loss of most of the soil A horizon and hence most of the soil organic matter and nutrient capital, and alteration of nutrient cycling processes (Nikiforoff 1959, Anderson 1988); (2) loss of extinction-prone perennial grasses (Mack and Thompson 1982, O'Connor 1991), which are the key climax

[1]School of Renewable Natural Resources, 325 Biological Sciences East Building, University of Arizona, Tucson, AZ 85721.
[2]Pacific Northwest Research Station, 1401 Gekeler Lane, LaGrande, OR 97850. Corresponding author.

dominants in similar subalpine landscapes throughout the West, and were thought by Sampson (1919) to have dominated the pristine vegetation here.

Although both explanations for the apparent static condition of soil-plant systems on the Wasatch summer range have merit, we focus on the former in this paper. More specifically, we hypothesized that losses of soil phosphorus (P) and/or sulfur (S) following the period of destructive grazing and erosion have diminished levels of one or both nutrients to the extent that accumulation of organic C and N to pre-degradation levels has been impeded (Walker and Adams 1958, Cole and Heil 1981). This in turn has limited soil development during range recovery. An alternative hypothesis was that neither P nor S was limiting relative to other elements, but that soil loss was so extensive that productive potential is now largely governed by the amount of remaining soil (i.e., A and B horizon). Under either hypothesis, regaining climax conditions of the former ecosystem would seem to require soil formation over a very long time to reestablish the original steady-state soil profiles characteristic of the pre-1870 climax soil-plant-nutrient system (Olsen 1958, Jenny 1980).

STUDY AREA

The study area is centrally located on the Wasatch Plateau about 17 km east of Manti, Utah. The area extends south 7 km from near the Alpine Station along Skyline Drive (Road 139) to Snow Lake. The long, narrow plateau is oriented approximately north and south with riblike ridges extending east and west. The plateau top is gently rolling, but gradient steepens (up to 65%) on slopes of east–west drainages. Average annual precipitation is about 840 mm; 2/3 of this falls as snow between November and April. Precipitation averages 173 mm during summer months (June through September) but varies considerably. Mean annual temperature is about 0°C (Ellison 1954). During the growing season (May through October), average maximum temperature is 21°C; average minimum is –5°C (Ellison 1954).

Soil parent materials are of the Flagstaff formation (Stanley and Collinson 1979) that outcrop over about 7200 km^2 in central Utah (Schreiber 1988). The dominant lithology is freshwater lacustrine limestone and calcareous shales with minor interbeds of sandstone, oil shale, conglomerate, gypsum, and volcanic ash (Weber 1964, Schreiber 1988). Soils of the plateau are mostly fine, mixed argic Cryoborolls, but lithic, pachic, and vertic Cryoborolls also are present. They are shallow to moderately deep; subsoils are silty clays or clay loams. Thickness of the A horizon averages just 4 cm; that of the B horizon averages 52 cm (range 30–74 cm). Based on typical profile descriptions (H.K. Swenson, Natural Resources Conservation Service, Boise, ID, personal communication), these relative horizon thicknesses indicate that much of the original A horizon was lost by wind and water erosion following the period of unrestricted grazing prior to 1903.

Vegetation of the Wasatch Plateau is chiefly herbaceous, but patches of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occupy steep northerly exposures of east–west ridges and dot the plateau landscape. Because remnants of pristine vegetation do not exist (Ellison 1949, 1954), opinions differ regarding its exact character. Ellison (1954) described the original herbaceous community as mixed-upland herb dominated by tall forbs, while Sampson (1919) considered wheatgrasses (*Agropyron* spp.) the primary climax dominants.

METHODS

The original strategy for testing the hypotheses was a comparative analysis of paired eroded and uneroded soil-plant systems at various locations. However, after an exhaustive search, it was apparent that grazing use of this summer range had been so complete during the period of devastation that uneroded sites were nonexistent, even on plateaus isolated by steep terrain that we believed would limit access to livestock.

Instead, we selected 6 topographically separated locations, mostly small knolls, and sampled soil and plant attributes on up to 4 aspects. All 6 locations had a similar grazing history until the 1930s. Since then Elk Knoll (EK) and Alpine Cattle Pasture (CP) have been protected from livestock. Ideally, this would give us an array of site conditions that would permit differentiation among locations and aspects based on soil, parent material, and vegetation properties, and permit determination of key variables influencing herbage composition and production on the summer range.

On each location we attempted to restrict aspect sampling points to a single parent material stratum; hence, elevation among aspects was near constant. However, this was probably futile. Because individual parent material strata were usually very thin (≤0.5 m; Klemmedson and Tiedemann 1994), there was little confidence in sampling the same parent material among all aspects of a location. All locations were within 7 km of each other. Northeast, SE, SW, and NW aspects were sampled on Elk Knoll (EK; elevation 3116 m) and a knoll adjacent to Snow Lake (SL; elevation 3133 m). Two aspects were sampled on Trail Ridge (TR; elevation 3216 m), Skyline Drive (SD; elevation 3200 m), and Alpine Cattle Pasture (CP; elevation 3066 m); a single aspect was sampled on South Knoll (SK; elevation 3109 m). Slope gradient was 10–30% among aspects on SL; gradients were <5% on other locations.

We sampled at selected aspects from randomly located soil pits and vegetal-litter-cover plots. Soil pits were dug and profiles described by standard terminology. Single samples of known volume were taken from each horizon (3–5 above the C or R horizon) for laboratory analysis. Herbage and litter were sampled in 6 randomly located 0.5-m^2 plots near each pit. Basal cover of litter, bare ground, and rock, and foliar cover by species were visually estimated; mass of grasses, forbs, and litter was determined by harvesting each component separately, followed by oven-drying (70°C) and weighing.

For chemical analyses we air-dried soils, sieved them to remove the >2-mm fraction, and then ground them to pass a 150-µm sieve. Samples were analyzed for total C by dry combustion (Nelson and Sommers 1982) in a LECO high-frequency induction furnace (LECO Corp., St. Joseph, MI). Organic C (C_o) of soils was determined by difference after determining carbonate by a gasometric method (Dreimanis 1962). Total N (N_t) was determined by semi-micro-Kjeldahl (Bremner and Mulvaney 1982) and total S (S_t) by dry combustion in the LECO high-frequency induction furnace (Tiedemann and Anderson 1971). Total soil P (P_t) was determined using ascorbic acid color development (Olsen and Sommers 1982) following hydrofluoric acid digestion (Bowman 1988). Inorganic P (P_i) was determined with the same color development on samples ignited at 550°C for 2 h (Olsen and Sommers 1982), while organic P (P_o) was determined by difference. Available nutrients (X_{av}) were determined as follows: P by ascorbic acid color development following 0.5 M sodium bicarbonate extraction (Olsen and Sommers 1982), N by steam distillation of 2 N KCl extracts (Keeney and Nelson 1982), and S with 1:1 water extracts, followed by ion chromatography (Dick and Tabatabai 1979).

To facilitate comparison among sites and aspects, we summarized soil horizon data and expressed the data for the 0- to 15-cm soil layer and for the entire solum. The data were analyzed by 2 ANOVAs: 1 for EK and SL knolls with data for all 4 aspects, the 2nd with data from all 6 locations, where the number of aspects sampled was unequal. In the latter ANOVA the interaction term was calculated using data only for EK and SL locations. Backward (stepwise) multiple regression analysis was used to relate herbage yield and composition to soil surface and 0- to 15-cm soil layer properties.

RESULTS AND DISCUSSION

Location and Aspect Differences

VEGETATION AND SOIL COVER.—Analysis of variance for all locations showed significant differences among locations for 6 attributes of vegetation and cover at the $P \leq 0.05$ level (Table 1). Of these, forb yield was the only attribute that also differed significantly among aspects (Table 1); it was highest on NW aspects and lowest on NE and SE aspects (Table 2). The significant location response of forb composition (by foliar cover) must be qualified because of the significant Location × Aspect interaction (Table 1). Forb composition responded differently to aspect at EK and SL locations, especially on SE and SW aspects (Table 2). This response may, at least in part, be influenced by parent material at the SL location. In a companion study (Klemmedson and Tiedemann 1998), parent material was highly associated with vegetal properties.

Based on values for the 6 vegetation and cover attributes discussed above, the locations appear to form 2 distinct groupings (Fig. 1). The EK, CP, and SK locations were similar for

TABLE 1. Probability values from analysis of variance for all locations, and for Elk Knoll (EK) and Snow Lake (SL) locations alone.

	Probability values				
	All locations			EK and SL	
Variables	Location	Aspect	L × A	Location	Aspect
VEGETATION AND SURFACE COVER					
Total yield (g/m^2)	0.033	NS	NS	NS	NS
Forb yield (g/m^2)	<0.001	0.038	NS	0.004	NS
Grass composition (%)	0.036	NS	NS	0.090	NS
Forb composition (%)	0.034	NS	0.050	0.090	NS
Bare ground (%)	0.006	NS	NS	NS	NS
Rock cover (%)	0.029	NS	NS	0.004	NS
SURFACE SOIL, 0–15 CM					
Organic C (kg/m^2)	0.071	NS	NS	0.053	NS
Available N (g/m^2)	<0.001	0.099	NS	NS	NS
Total P (g/m^2)	0.009	0.010	NS	0.002	0.049
Inorganic P (g/m^2)	0.010	0.069	NS	0.013	NS
Organic P (% of total)	0.013	NS	0.010	0.047	NS
Total K (kg/m^2)	NS	NS	NS	0.019	NS
C_o/P_t	0.004	NS	NS	0.005	NS
C_o/S_t	0.007	NS	NS	0.001	NS
N_t/P_t	<0.001	NS	NS	0.001	NS
N_t/P_o	0.002	NS	NS	0.138	NS

TABLE 2. Influence of aspect on forb yield, and interaction of location and aspect on forb composition by foliar cover.

	Aspect				
	NE	SE	SW	NW	LSD*
Forb yield (g/m^2)	75	76	98	128	24
Forb composition (%)					17
Elk Knoll	67	84	87	90	
Snow Lake	61	53	28	72	

*$P < 0.05$.

composition of grasses and forbs, less so for cover of bare ground and rocks, and differed in herbage yield (Fig. 1). Yield of forbs and total herbage for the EK and CP locations was similar, and much greater than that for the SK location. Herbage yield at all 3 locations was dominated by forbs (>80% of yield and composition). These locations had little exposed rock (<5%) and moderate amounts of bare ground (13–26%).

The SL, TR, and SD locations form the 2nd group. They were similar to each other for most attributes, especially yield of forbs and composition of grasses and forbs (Fig. 1). They had significantly lower total herbage yield than the EK and CP locations and vegetal composition was about equally divided between grasses and forbs. These locations (SL, TR, and SD) all had large amounts of bare ground and exposed rock (Fig. 1).

The 6 locations break out into the same groupings based on species composition. Of the 25 species comprising at least 3% of the composition (Table 3), only 2 grasses (*Agropyron trachycaulum* and *Stipa lettermani*) and 1 forb (*Achillea millefolium*) occurred on all 6 locations. Composition of these 3 species was similar among the SL, TR, and SD locations, and from 2.0- to 6.6-fold higher than that for the EK, CP, and SK locations. The 2 groups of

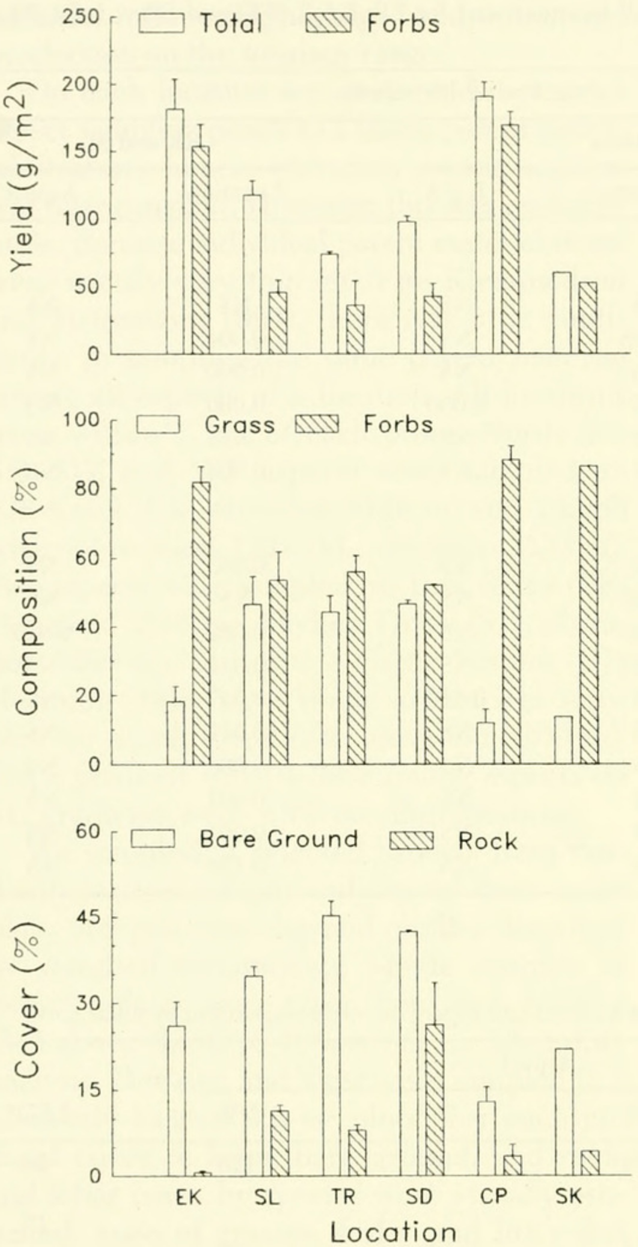

Fig. 1. Effect of location on yield of forbs and total vegetation, composition (by foliar cover) of grasses and forbs, and cover of bare ground and rocks.

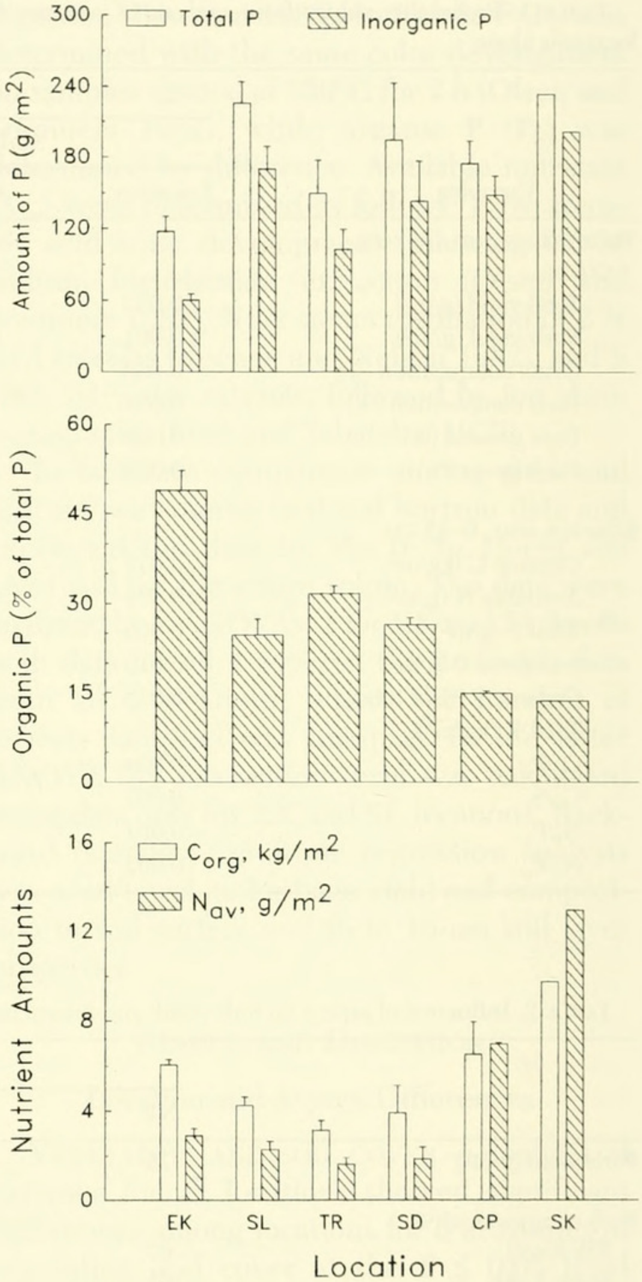

Fig. 2. Effect of location on amounts of total and inorganic P, percentage organic P, and amounts of organic C and available N in soils.

locations also differed in distribution of several forbs. Six species (*Aster foliaceus* v. *canbyi*, *Erigeron speciosus*, *Geranium fremontii*, *Ligusticum porteri*, *Penstemon rydbergii*, and *Potentilla gracilis*) were found only on the EK, CP, and SK locations (at least 2 of the 3 locations), while 2 species (*Artemisia ludoviciana* v. *incompta* and *Cymopterus lemmonii*) occurred only on the SL, TR, and SD sites (Table 3). In a companion study on the SL location (Klemmedson and Tiedemann 1998), *C. lemmonii* was highly associated with rocky sites with shallow soils of low nutrient content.

SOIL PROPERTIES.—Nine properties of the 0- to 15-cm soil layer differed significantly among the 6 locations (Table 1). Differences were significant at the $P \leq 0.01$ level for N_{av}, P_t, P_i, and the C_o/P_t, C_o/S_t, and N_t/P_t ratios, at the $P \leq 0.05$ level for percentage P_o, and at $P \leq 0.10$ for C_o. In the case of P_o content as a percentage of P_t, there was a significant L × A interaction (Table 1): P_o was markedly higher at the EK than the SL location for all aspects except SW.

Results of the analysis of variance for EK and SL locations alone (Table 1) were similar to that for all locations, with 2 exceptions. These 2 locations did not differ significantly in

TABLE 3. Species composition (%) at 6 knoll locations[a].

Vegetal component	Knoll location[b]					
	EK	SL	TR	SD	CP	SK
GRASSES AND GRASSLIKE						
Agropyron trachycaulum	7.6	10.5	13.1	8.9	3.6	3.4
Alopecurus pratensis						3.4
Carex microptera	3.6					
Stipa columbiana		6.7				
Stipa lettermani	3.8	28.2	30.5	36.6	5.2	6.0
Others	3.2	1.0	0.6	2.7	3.0	0.8
Total	18.2	46.4	44.2	48.2	11.8	13.6
FORBS AND SHRUBS						
Achillea millefolium ssp. *lanulosa*	8.4	12.6	15.0	11.3	5.8	5.6
Artemisia ludoviciana v. *incompta*		18.8	4.7	19.7		
Aster foliaceus v. *canbyi*	13.6					
Astragalus miser v. *oblongifolius*			3.0			
Castilleja sulphurea					4.6	5.2
Cymopterus lemmonii		5.2	9.8	10.6		
Erigeron speciosus	5.3				4.9	3.4
Erigeron ursinus			8.2			
Geranium fremontii	13.5				22.4	
Lesquerella utahensis				3.3		
Ligusticum porteri	5.2				8.2	
Penstemon rydbergii	10.9				4.4	3.6
Potentilla glandulosa			3.4			
Potentilla gracilis	3.1				10.8	
Solidago parryi						55.2
Swertia perennis	3.0					
Taraxacum officinale		4.6	6.5			
Valeriana occidentalis					4.2	3.6
Vicia americana v. *americana*		6.4			4.6	
Vicia nuttallii v. *nuttallii*					5.8	
Others	18.8	6.0	5.2	6.9	12.6	9.8
Total	81.8	58.6	55.8	51.8	88.3	86.4

[a]Based on foliar cover; species with <3% composition not listed.
[b]See text for names and descriptions of locations.

N_{av}, but they did differ in total K. Moreover, there was a significant L × A interaction for P_t. Although P_t was higher at SL than at EK (Fig. 2), the absolute and proportional differences were a function of aspect.

For soil properties, the 6 locations did not break out into the 2 groups observed for vegetation and cover attributes. Those groupings were apparent only for 1 of the 9 soil properties (C_0/P_t ratio) found to differ among locations (Fig. 3). Analysis of data for variables of the entire solum added very little information to that shown for the 0- to 15-cm soil layer and hence are not shown here.

Vegetation-Soil Relations

The marked differences described above in vegetal attributes and soil properties among locations caused us to pursue further soil-vegetation relations that might explain vegetational differences among locations (Fig. 1, Table 3) and give clues to the seral plateau these systems have been in for the past 50 yr. Simple linear regression relating vegetal attributes with soil properties, especially those shown to be significant in Table 1, indicates that grasses and forbs, as groups, responded differently, but consistently, to these variables (Table 4). In fact, for each independent variable shown in this table for regressions with herbage yield and composition as dependent variables, the regression coefficients for grasses were always opposite in sign to that for forbs. Certainly, this was not the case for all independent variables we sampled, but for the large majority the trend was very noticeable.

In a companion study at the SL location (Klemmedson and Tiedemann 1998), the dominant grass (*Stipa lettermani*) and forb (*Cymopterus lemmonii*) were oppositely related for

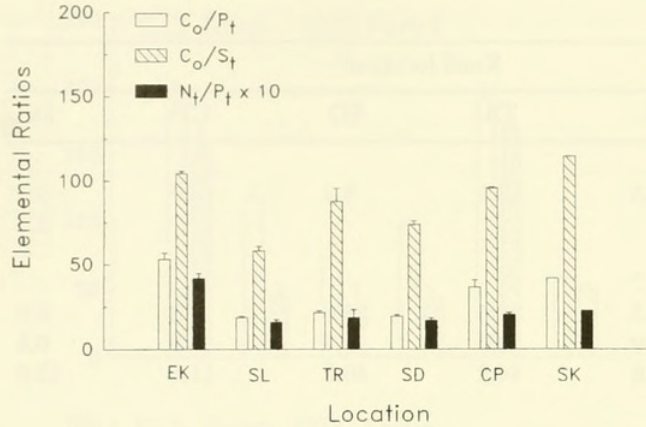

Fig. 3. Effect of location on elemental ratios of soil.

every variable sampled. But, for groups of grasses and forbs comprising many species (Table 3), it is remarkable that these groups would respond in an opposite manner so consistently to various growth (soil/site) parameters, although not always with high r-values (Table 4). That correlation coefficients associated with specific independent variables in Table 4 were not high, as a rule, is a reflection of the individuality of species within grass and forb groups in response to location and aspect. Figure 4 illustrates this individuality of 2 grasses and 2 forbs in their response to C_0/P_t and C_0/S_t, variables that were both highly correlated with grass and forb composition (Table 4). Contrasting responses of grass and forb groups also have been observed by Huenneke et al. (1990) in short-term fertilization experiments on serpentine soils. Within vegetal groups having common properties, species responded to experimental treatments in an individualistic manner. Also, Chapin and Shaver (1985) observed this kind of species-community behavior in response to manipulation of environment in tundra.

Of those variables one would ordinarily associate with soil fertility, only C_0 and the 2 element ratio variables were correlated with yield and composition (Table 4). The high r-values for percentage litter cover and rock cover are at first puzzling. However, when one considers the extent of correlation usually observed among soil-plant-litter properties, both positively and negatively, high r-values for soil surface variables (Table 4) are not surprising. Moreover, these soil surface variables may be expressing the influence of soil physical properties that we did not sample, but

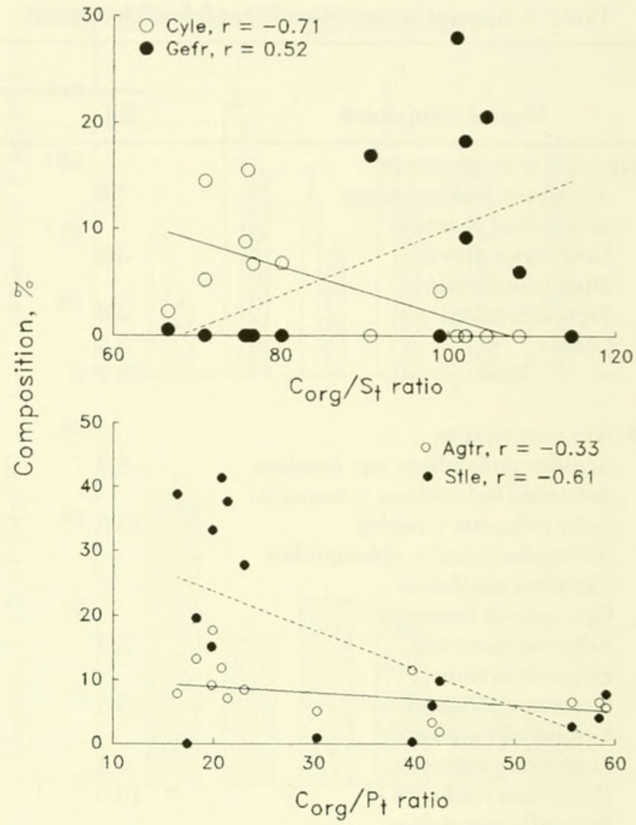

Fig. 4. Relationship of composition (by foliar cover) of *Cymopterus lemmonii* and *Geranium fremontii* to C_0/S_t ratio and composition of *Agropyron trachycaulum* and *Stipa lettermani* to C_0/P_t ratio.

which may have significantly influenced vegetal yield and composition.

Table 5 summarizes our attempt to predict herbage yield and composition with 2-variable equations using backward multiple regression. Overall, percentage rock cover was the most efficient predictor of yield and composition of both grass and forbs, based on standardized regression coefficients. Percentage litter cover and bare ground were about equal as predictors of total yield. P_0 was as efficient as soil surface features only in the grass yield equation. When a 3rd variable was allowed in the equation (3-variable equations not shown), P_0 filled that role in 4 of 5 cases, based on variation explained. In the 3-variable grass yield equation, C_0 became the 3rd and most efficient variable. That variables portraying soil surface features would appear as the most efficient predictors of vegetal yield and composition in multiple regression is not surprising in view of results from simple regression (Table 4) and suggests a high degree of intercorrelation with soil properties more commonly associated with productivity.

TABLE 4. Contrasting regression relations between yield and composition of grasses and forbs and several independent variables.

Dependent variables	Independent variables	Regression coefficient		Correlation coefficient	
		Grass	Forbs	Grass	Forbs
Yield (g/m^2)	Organic C (g/m^2)	−7.176	25.158	−0.43	0.68**
	Total N (g/m^2)	−0.090	0.234	−0.30	0.40
	Total P (g/m^2)	0.146	−0.416	0.27	−0.40
	Total S (g/m^2)	−0.431	0.799	−0.25	0.24
	C_o/P_t	−1.273	2.895	−0.63*	0.73**
	N_t/P_o	−6.627	14.116	−0.64*	0.67**
	Rock cover (%)	3.356	−9.188	0.58*	−0.81**
	Litter cover (%)	−0.051	4.123	−0.13	0.76**
Composition[a]	Organic C (g/m^2)	−5.993	5.940	−0.54*	0.54*
	Total N (g/m^2)	−0.079	0.076	−0.49	0.49
	Total P (g/m^2)	0.087	−0.092	0.28	−0.29
	Organic P (g/m^2)	0.435	−0.449	0.42	−0.43
	C_o/P_t	−0.881	0.890	−0.74**	0.74**
	C_o/S_t	−0.820	0.830	−0.69**	0.70**
	Rock cover (%)	2.686	−2.754	0.79**	−0.80**

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
[a]Based on foliar cover.

TABLE 5. Statistics from backward multiple regression predicting herbage yield and composition (based on foliar cover) with 2-variable equations.

Herbage component	Variables	Standardized coefficient	Probability of significant F	R-square
YIELD				
Total	Regression		0.002	0.72
	Litter cover	0.238	0.001	
	Bare ground	−0.216	0.067	
Grass	Regression		0.026	0.52
	Rock cover	0.493	0.024	
	Organic P	0.454	0.085	
Forbs	Regression		0.001	0.76
	Litter cover	0.408	0.001	
	Rock cover	−0.553	0.021	
COMPOSITION				
Grass	Regression		0.007	0.63
	Litter cover	−0.094	0.016	
	Rock cover	0.730	0.015	
Forbs	Regression		0.005	0.64
	Litter cover	0.092	0.013	
	Rock cover	−0.744	0.012	

We demonstrated strong association between grass- versus forb-dominated vegetation and several soil nutrient and surface soil properties. On the whole it appears that forbs responded positively to variables generally associated with better growing conditions, and the opposite for grasses. Moreover, results demonstrate marked differences among the 6 study locations based on these soil-plant relations. Although vegetation was strongly associated with P, and to a lesser extent S, it seems premature to accept the primary hypothesis regarding the importance of P and S. The opposite relationship of grasses and forbs to depth of A

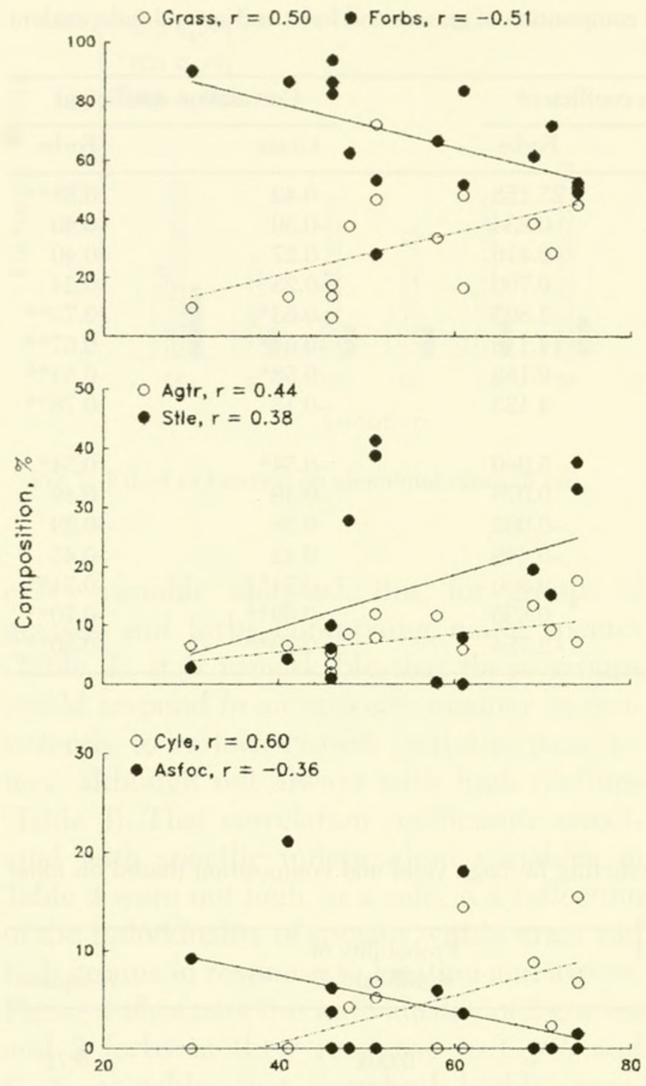

Fig. 5. Effect of thickness of A + B horizon on composition (by foliar cover) of grasses, forbs, *Agropyron trachycaulum*, *Stipa lettermani*, *Cymopterus lemmonii*, and *Aster foliaceus* v. *canbyi*.

and B horizon (Fig. 5) supported the alternate hypothesis that plant attributes are governed by depth of soil remaining after the period of destructive grazing. It is also apparent from the differential response of individual species within each group (Fig. 5) that these relationships are not straightforward.

We believe soil and plant attributes that distinguish the 6 locations were primarily a reflection of the parent materials and the soil that remained (mainly B horizon) after many years of destructive grazing and severe erosion. Differences among soils, which in this case were chiefly a function of differences in composition of parent material, were manifested in soil-vegetation relationships established here. All 6 sites were unprotected during the period prior to 1905, and they appear to have suffered more or less equally, losing 50–90% of the A horizon (Klemmedson and Tiedemann 1994). Grazing over the past 80 yr differed among the 6 locations; EK and CP have been reasonably well protected since the 1930s. But the impact of differential grazing since 1905, though marked in the case of EK and CP locations, appears to be small compared to the differences among sites coupled with the earlier loss of so much of their productive capacity through erosion.

CONCLUSIONS

Although we demonstrated strong relationships among several soil and vegetal properties, cause-and-effect relationships were not forthcoming from this information. Comparisons with undisturbed areas would perhaps have provided such linkages. Nonetheless, it is apparent that yield and composition of vegetation were closely tied to soil properties. Of the physical properties, rock cover was the best predictor of yield and composition of grasses and forbs. Litter cover was the best vegetal attribute for predicting forb yield and composition. Of the soil chemical characteristics, the C_o/P_t ratio was the best predictor of forb and grass yield and composition.

The opposite response of grasses and forbs as groups, as indicated by regression coefficients, to all measured attributes suggests that these 2 groups occupy different seral positions in successional development of this area. Their roles in successional dynamics are not clearly defined and will require more careful study of their responses to soil development. Contrasting responses of individual species within plant groups (Figs. 4, 5) suggest the need to focus on species-level responses. In a companion study we are attempting to do this by examining foliar cover response to fertilization with 5 combinations of N, P, K, and S for about 100 species over a 5-yr period.

Depth of remaining soil, over 90% B horizon, has not been emphasized in earlier studies of this area but may be an important determinant in the composition of grasses and forbs as plant groups. Depth of B horizon varied widely among sites and locations and may be a primary reason that location was such an important factor in the analysis.

ACKNOWLEDGMENTS

This research was supported by Grants 85-CRSR-2-2717 and 91-38300-6156, Range Research Grant Program, USDA-CSRS. The authors gratefully acknowledge the Shrub Improvement and Revegetation Project, Intermountain Research Station, Provo, Utah, for providing facilities for this research; field assistance of Gary Jorgensen, range technician, Intermountain Research Station, and Dr. Clyde Blauer, professor, Snow College, both of Ephraim, Utah; and laboratory analysis by Justine McNeil, University of Arizona. We thank Dr. Paul Doescher, Oregon State University, and Dr. Richard Everett, Pacific Northwest Research Station, for reviews of the manuscript. We also thank peer reviewers selected by the Great Basin Naturalist for their helpful suggestions.

LITERATURE CITED

ANDERSON, D.W. 1988. The effect of parent material and soil development on nutrient cycling in temperate ecosystems. Biogeochemistry 5:71–79.

BOWMAN, R.A. 1988. A rapid method to determine total phosphorus in soils. Soil Science Society of America Journal 52:1301–1304.

BREMNER, J.M., AND C.S. MULVANEY. 1982. Nitrogen—total. Pages 595–624 *in* A.L. Page, editor, Methods of soil analysis, part 2. 2nd edition. Agronomy Monograph 9. American Society of Agronomy and Soil Science Society of America, Madison, WI.

CHAPIN, F.S., III, AND G.R. SHAVER. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66: 564–576.

COLE, C.V., AND R.D. HEIL. 1981. Phosphorus effects on terrestrial nitrogen cycling. Ecological Bulletin (Stockholm) 33:363–374.

CROFT, A.R. 1967. Rainstorm debris floods. Arizona Agricultural Experiment Station, Tucson. 36 pp.

DICK, W.A., AND M.A. TABATABAI. 1979. Ion chromatographic determination of sulfate and nitrate in soils. Soil Science Society of America Journal 43:899–904.

DREIMANIS, A. 1962. Quantitative gasometric determination of calcite and dolomite by using Chittick apparatus. Journal of Sedimentary Petrology 32:520–529.

ELLISON, L. 1949. Establishment of vegetation on depleted subalpine range as influenced by microclimate. Ecological Monographs 19:97–121.

______. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecological Monographs 24:89–124.

HUENNEKE, L.F., S.P. HAMBURG, R. KOIDE, H.A. MOONEY, AND P.M. VITOUSEK. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478–491.

JENNY, H. 1980. The soil resource: origin and behavior. Springer-Verlag, New York. 377 pp.

JOHNSON, H.B. 1964. Changes in vegetation of two restricted areas of the Wasatch Plateau, as related to reduced grazing and complete protection. Unpublished master's thesis, Brigham Young University, Provo, UT.

KEENEY, D.R., AND D.W. NELSON. 1982. Nitrogen—inorganic forms. Pages 643–698 *in* A.L. Page, editor, Methods of soil analysis, part 2. 2nd edition. Agronomy Monographs 9. American Society of Agronomy and Soil Science Society of America, Madison, WI.

KLEMMEDSON, J.O., AND A.R. TIEDEMANN. 1994. Soil and vegetation development in an abandoned sheep corral on degraded subalpine rangeland. Great Basin Naturalist 54:301–312.

______. 1998. Lithosequence of soils and associated vegetation on subalpine range of the Wasatch Plateau. Research Note PNW-RN-524. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. 16 pp.

LAYCOCK, W.A. 1991. Stable states and thresholds of range condition on North American rangelands. Journal of Range Management 44:427–433.

LEWONTIN, R.C. 1969. The meaning of stability. Brookhaven Symposia in Biology 22:13–24.

MACK, R.N., AND J.N THOMPSON. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757–773.

MEEUWIG, R.O. 1960. Watersheds A and B: a study of surface runoff and erosion in the subalpine zone of central Utah. Journal of Forestry 58:556–560.

NELSON, D.W., AND L.E. SOMMERS. 1982. Total carbon, organic carbon and organic matter. Pages 539–580 *in* A.L. Page, editor, Methods of soil analysis, part 2. 2nd edition. Agronomy Monographs 9. American Society of Agronomy and Soil Science Society of America, Madison, WI.

NIKIFOROFF, C.C. 1959. Reappraisal of the soil. Science 129:186–196.

O'CONNOR, T.G. 1991. Local extinction in perennial grasslands: a life-history approach. American Naturalist 137:753–773.

OLSEN, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Botanical Gazette 119:125–170.

OLSEN, S.R., AND L.E. SOMMERS. 1982. Phosphorus. Pages 404–430 *in* A.L. Page, editor, Methods of soil analysis, part 2. 2nd edition. Agronomy Monographs 9. American Society of Agronomy and Soil Science Society of America, Madison, WI.

REYNOLDS, R.V.R. 1911. Grazing and floods: a study of conditions in the Manti National Forest, Utah. U.S. Forest Service Bulletin 91. 16 pp.

SAMPSON, A.W. 1919. Plant succession in relation to range management. U.S. Department of Agriculture Bulletin 791. 76 pp.

SAMPSON, A.W., AND L.H. WEYL. 1918. Range preservation and its relation to erosion control on western grazing lands. U.S. Department of Agriculture Bulletin 675. 35 pp.

SCHREIBER, J.F., JR. 1988. Final report on the Flagstaff Limestone (Paleocene–Early Eocene) in the Manti–LaSal National Forest, east of Manti-Ephraim, Sanpete County, Utah. Unpublished report, Department of Geosciences, University of Arizona, Tucson.

STANLEY, K.O., AND J.W. COLLINSON. 1979. Depositional history of Paleocene–Lower Eocene Flagstaff Limestone and coeval rocks, central Utah. American Association of Petroleum Geologists Bulletin 63:311–323.