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Vegetation Patterns on Limestone and Acid Parent Materials in the Garnet Mountains of Western Montana[2]

Abstract

Parent material has a strong influence on the distribution and coverage provided by individual species and life forms. *Pinus contorta* var. *latifolia* and the *Vaccinium* species, in particular, are poorly represented over limestone substrates. Classification of the vegetation on each substrate by habitat types also reveals marked differences. Nomenclature follows that of Hitchcock and Cronquist 1973, except where authorities are given.

Introduction

Parent material plays a major role in the development of a soil and its physical and chemical properties. Limestone materials have a particularly significant influence on soil morphology which results from their high base saturation and calcium content, their tendency to produce alkaline soils, and their solubility in weak acids. Because soil is the medium in which most plants grow, parent material influences their growth and distribution.

The objective of this research was to quantify the differences in plant communities on soils developed from limestone as compared to those on granite and quartzite. Particular attention was paid to the distribution of *Pinus contorta* var. *latifolia,* an important tree species in the northern Rocky Mountains, and the *Vaccinium* species.

The influence of parent material on soil properties often causes abrupt differences in vegetal cover and growth rates between adjacent soils formed from different rocks (Bamberg and Major, 1968). Differences have been shown to be particularly evident on serpentine and limestone soils[3] in contrast to soils formed from acid rocks, such as granite (Whittaker *et al.,* 1954; Mooneye *et al.,* 1962; Whittaker and Niering, 1968). The literature pertains almost exclusively to trees. The effects of parent material on undergrowth plants and life forms are scarcely mentioned. No studies have been published on the forest vegetation of limestone soils in western Montana.

Some tree species, such as *Juniperus scopulorum* in the western United States and *J. virginiana* in the Southeast, are associated with and are very tolerant of soils derived from limestone bedrock (Lutz and Chandler, 1946). *Pinus contorta* in the western

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[3] For the sake of brevity, the following expressions will be considered synonymous in this report: soils derived from limestone bedrock, limestone soils, limestone-derived soils. Similarly for limestone vegetation, which corresponds to vegetation growing on soils derived from limestone bedrock.

United States and *Quercus robur* L. on the British Isles, on the other hand, are poorly represented on these soils; *Pseudotsuga menziesii* var. *glauca* and *Fraxinus excelsior* L., respectively, generally replace them in the plant community overlying this substrate (Eyre, 1963; Holdorf, 1976).

In the Big Horn Mountains of Wyoming, *Pinus contorta* is clearly associated with granitic substrates and rarely occurs on limestone, whereas the reverse is true with *Pseudotsuga menziesii* (Despain, 1973). A similar relationship between vegetation and substrate is noted by Patten (1963) in the Madison Range of Montana where *Pseudotsuga menziesii* is associated with limestone formations and *Pinus contorta* with volcanic rocks. In Gunnison County, Colorado, Langenheim (1962) reports that *Pinus contorta* occurs only on granitic or coarse clastic parent materials and infrequently on limestone.

Soil chemical and physical factors (especially those related to moisture and phosphorus deficiency) have been reported to be possible causes for species-substrate relationships. The reasons for different species tolerances of limestone and nonlimestone soils, however, are complex and incompletely understood (Goldin, 1976).

Description of Study Area

The study area encompasses about 2600 ha of forest land in the northwestern part of the Garnet Mountains (lat. 45°50′N, long. 113°20′W) in western Montana about 50 km east of Missoula (Fig. 1).

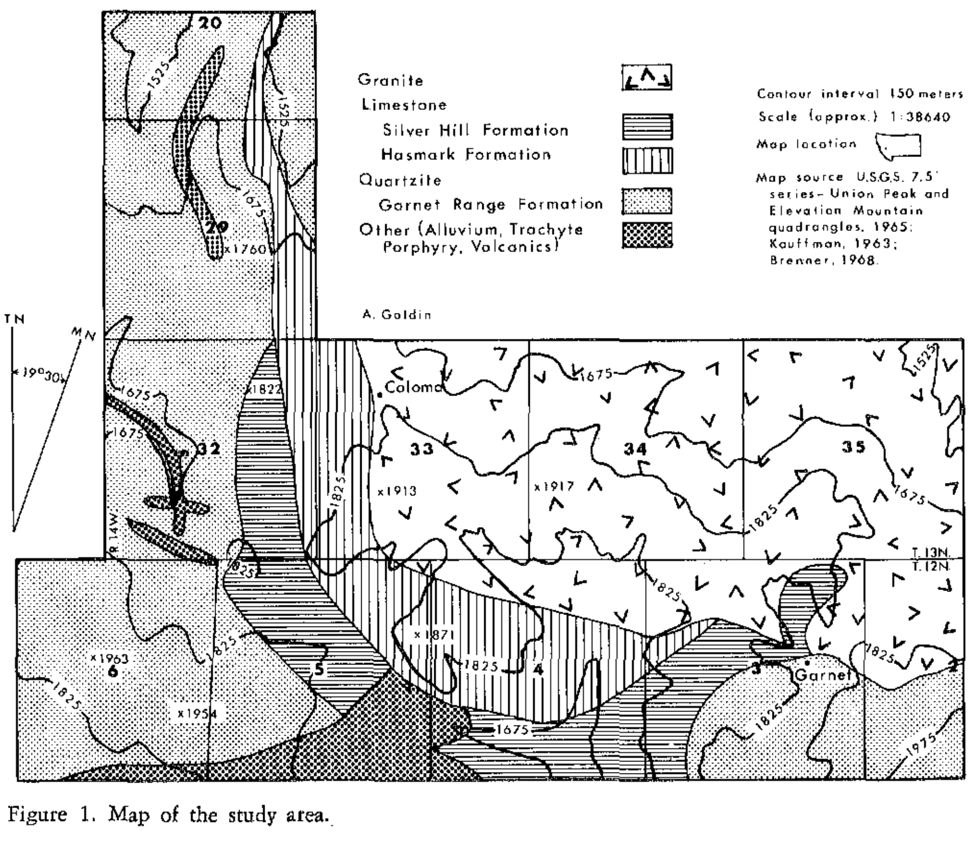

Figure 1. Map of the study area.

Three types of materials underlie the study area: igneous rocks of granite and granodiorite stocks; Cambrian limestones, dolomites, and marbles of the Silver Hill and Hasmark Formations; and Precambrian micaceous quartzites of the Garnet Range Formation (Kauffman, 1963; Brenner, 1968).

The area has a mean annual temperature of about 2°C. Average annual precipitation is approximately 60 cm, which occurs mostly as snow between October and May.

A mosaic of vegetation has resulted from disturbance factors (fire, logging, mining) and site factors (topographic differences and geologic material). The range of vegetational composition extends from the dry *Pseudotsuga menziesii* habitat types on drier slopes over limestone parent material to the temperate, moist *Abies lasiocarpa* habitat types on granite and quartzite (Pfister *et al.,* 1974).

Methods

Plot establishment: General plot locations on the three substrates were predetermined onto topographic maps based on the following three topographic factors: aspect, elevation, and slope steepness. These locations were determined by stratified random selection from geologic maps (Kauffman, 1963; Brenner, 1968), and the 7.5 minute Union Peak and Elevation Mountain United States Geological Survey topographic maps.

Due to the variability in landscape and the lack of complete constancy of these factors, two aspect groupings, three elevational ranges, and three slope steepness categories were established for each parent material. The interaction of these three factors produced 18 combinations for each substrate. However, since no limestone was present on south slopes below 1675 m on the study area, no data were collected on any parent material in this aspect-elevation grouping. The sample number on each substrate was thus reduced to 15 and the total number of plots to 45.

Ground checking during the summer of 1975 more accurately located the plot centers from the approximate map locations. Once situated at the approximate position, a random and representative sample plot center was established with special precautions to avoid edge effects, obvious ecotones and microsites, dense clumping, and obvious disturbance.

Field procedures: The general field procedures for vegetational sampling and habitat classification follow those of Pfister *et al.* (1974). On each 375-m^2 circular plot the following data were recorded: 1) location, 2) aspect, 3) elevation, 4) slope steepness, 5) canopy coverage class for tree species in two diameter groupings 10 cm or more at breast height (1.4 m), and those less than 10 cm, and 6) canopy coverage class for each vascular undergrowth plant species. Coverage classes for trees and undergrowth vegetation are as follows:

Coverage Class	Percentage of Area Covered
T	0-1
1	1-5
2	5-25
3	25-50
4	50-75
5	75-95
6	95-100

A soil pit was dug near the center of each plot and described according to standard procedures (Soil Survey Staff, 1951). Color notation followed the Munsell system. Samples of each horizon from six pits, which represented the model profile by aspect on each substrate, were analyzed for particle-size distribution by the hydrometer method (Bouyoucos, 1951), and for the percentage of rock fragments (larger than 2 mm).

Office procedures: Association between species on each substrate was determined using the Student's t-test at the 95 percent significance level. The analysis of variance (F-test) was used to test the homogeneity of variance prior to conducting the t-test.

An Index-of-Similarity ordination was constructed to array the stands graphically based on the coverage class values for each plant species (Bray and Curtis, 1957). Most of the meaningful variation was accounted for in the x-axis, which was strongly related to the effects of substrate on vegetational composition. The y-axis was apparently weakly related to temperature. The stands, their habitat types, and the coverage class distribution of the prominent species were plotted on this ordination. End stands for the x-axis, a *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type on limestone, and an *Abies lasiocarpa/Linnaea borealis* habitat type on granite were chosen on the basis of 96 percent dissimilarity and relatively low total dissimilarities with the other stands, indicating that they were not highly unusual.

Results

Soils: The topographic criteria established for plot selection (aspect, elevation, and slope steepness) were subordinate in influence to parent material, which played the major role in the soil development process.

Limestone: The soils derived from limestone bedrock were medium-textured, gravelly, calcareous, and neutral to mildly alkaline. Three-fourths of these soils were classified in the Inceptisol order (Typic Cryochrepts); the rest were Entisols (Typic Cryorthents). A summary of the principal differences in soil properties among the three substrates is presented in Table 1.

TABLE 1. Summary of key morphological features of limestone, granite, and quartzite soils in the Garnet Mountains, Montana, based on 15 soil profiles described on each substrate.

Morphological feature	Substrate		
	Limestone	Granite	Quartzite
Average organic horizon thickness (cm)	2.3	4.0	4.0
Common horizon sequences	01-A1-B2-Cca 01-A1-Cca	01-A1-C 01-Bir-C 01-Bir-IIA2-C	01-A2-B2-C 01-A1-C 01-A2-Bir-C
Texture	silt loam	sandy loam	loam
Gravel content	gravelly to very gravelly	slightly gravelly	very gravelly
Soil reaction (solum)	neutral to mildly alkaline 6.5 - 8.0	medium to slightly acid 5.5 - 6.5	slightly acid to neutral 5.7 - 6.9
Calcareousness	Slight to strong on surface; strong at depth	none	none on surface; slight to strong at depth on some profiles

The organic horizon was significantly thinner on limestone-derived soils than on the soils from the other two substrates. The difference may result from the stimulative effect which calcium carbonate has on the decomposition of plant residues by maintaining alkaline soil conditions suitable for bacterial activity.

A modal limestone soil is described below. Most of the other soils described on this substrate had more rock fragments in the A1 horizon. Some of the profiles were more strongly calcareous near the surface and were thus more alkaline.

TYPIC CRYOCHREPT: LOAMY SKELETAL, MIXED CALCAREOUS, FRIGID
Habitat type: *Pseudotsuga menziesii/Calamagrostis rubescens*
Elevation: 1870 meters Aspect: 340°W Slope: 22 percent

Horizon	*Depth (cm.)*	*Description*
01	2 - 0	Decomposed forest litter from *Pseudotsuga menziesii* and undergrowth plants.
A1	0 - 10	Very dark brown (10YR 2.5/2) silt loam (5 percent gravel, 22 percent sand, 54 percent silt, 24 percent clay), dark grayish brown (10YR 4/dry); weak moderate granular breaking to weak fine blocky structure; soft, very friable, slightly sticky, slightly plastic; abundant fine roots; neutral (pH 6.8); very slightly calcareous; abrupt boundary.
B21	10 - 23	Light olive brown (2.5Y 5.5/4) very gravelly loam (53 percent gravel, 34 percent sand, 48 percent silt, 18 percent clay), yellowish brown (10YR 5/4, dry); weak medium blocky structure; soft, very friable, slightly sticky, slightly plastic; abundant fine roots; mildly alkaline (pH 7.4); slightly calcareous; clear boundary.
B22	23 - 38	Dark brown (10YR 4/3) gravelly silt loam (41 percent gravel, 40 percent sand, 51 percent silt, 9 percent clay), brown (10YR 5/3 dry); weak medium blocky structure; soft, very friable, slightly sticky, slightly plastic; common fine roots, mildly alkaline (pH 7.7); strongly calcareous; clear, irregular boundary.
Cca	38 - 93+	Pale brown (10YR 6/3) gravelly sandy loam (44 percent gravel, 63 percent sand, 26 percent silt, 11 percent clay), very pale brown (10YR 7/3, dry; massive; soft, very friable, slightly sticky, slightly plastic; few roots; moderately alkaline (pH 8.0); strongly calcareous.

Granite: Soils derived from granite were coarse-textured with scattered cobbles, noncalcareous, and of medium acidity. The granitic soils were classified as Entisols (Typic Cryorthents) and Inceptisols (Andic Cryochrepts). These two groups were very similar, differing mainly in the surface mineral horizon, which was a Bir in the Inceptisols and an A1 (ochric epipedon) in the Entisols. A thin, incipient A2 horizon overlaid most of the Bir horizons.[4]

A modal granitic soil is described below. In comparison to this profile, most of the granitic soils had a lower pH, a slightly thinner organic horizon, and a higher percentage of rock fragments.

ANDIC CRYOCHREPT: SANDY SKELETAL, MIXED, FRIGID
Habitat type: *Abies lasiocarpa/Linnaea borealis*
Elevation: 1820 meters Aspect: N10°W Slope: 9 percent

Horizon	*Depth (cm.)*	*Description*
01	8 - 0	Decomposed forest litter from *Abies lasiocarpa, Pinus contorta,* and *Pseudotsuga menziesii* and undergrowth plants.
Bir	0 - 31	Dark brown (7.5YR 4/4) sandy loam (20 percent gravel, 60 percent sand, 31 percent silt, 9 percent clay), brown (10YR 5/3,

[4] Different professional opinions exist regarding horizon nomenclature and soil classification of these volcanic ash soils. The one used here is in general usage in western Montana at this time.

		dry); weak fine subangular blocky structure, very soft, very friable, slightly sticky, slightly plastic, abundant fine roots; slightly acid (pH 6.5); clear, irregular boundary. Sporadic A2 horizon about 0.5 cm thick occurs above the Bir.
C	31-51+	Brown (10YR 5/3) gravelly coarse sandy loam (25 percent gravel, 72 percent sand, 18 percent silt, 10 percent clay), light brownish-gray (10YR 6/2, dry); massive; loose, very friable, nonsticky, nonplastic; few roots; neutral (pH 6.6).

Quartzite: The quartzitic soils were generally intermediate in morphology between the two soil types above: medium texture, very gravelly, generally noncalcareous, and slightly acidic. Two profiles were recognized on the quartzitic soils: 1) Inceptisols (Typic Cryochrepts) and Entisols (Typic Cryorthents) on the south slope and the drier north slope plots with a 01-A1(ochric)-C horizon sequence on the Entisols and an 01-A2-B2-C on the Inceptisols; and 2) Inceptisols (Andic Cryochrepts) on the moist north slope sites with an 01-A2(incipient)-Bir-C horizon sequence.

Soils of the first type were somewhat similar in description to the limestone soil above except for the noncalcareousness, loam texture, lighter colors, and more gravelly nature of the quartzitic soils. Soils of the second type were like the granitic profile above except for the finer texture and more gravelly nature of the quartzitic soils.

Vegetation

The vegetation on soils derived from limestone bedrock was in sharp contrast with that on granitic and quartzitic parent materials. The most obvious differences occurred in the distribution of the following species: *Pseudotsuga menziesii, Pinus contorta, Abies lasiocarpa, Vaccinium globulare, V. scoparium, Linnaea borealis, Xerophyllum tenax,* and *Calamagrostis rubescens.* Intersubstrate relationships were also contrasting in the coverage provided by each life form, in the relative canopy coverage, and in the habitat types associated with each substrate. The plant communities on limestone and granite displayed the greatest dissimilarity. They had no habitat types in common, and there was a wide separation in the ordination of the stands on these substrates (Tables 2, 3, and 4).

The vegetation on quartzite covered almost the entire range of habitat types and of the ordination. The more mesic sites corresponded to those on granite; those on dry sites were similar to ones on limestone.

Limestone: The overstory vegetation on the limestone substrate was dominated almost exclusively by *Pseudotsuga menziesii,* providing 34 percent relative coverage. This species generally occurred in open stands and accounted for over 99 percent of the tree coverage.

Shrubs constituted a very minor percentage of the floristic composition on limestone, accounting for only 7 percent relative coverage. Only two species were somewhat important: *Berberis repens* and *Symphoricarpos albus. Vaccinium globulare* and *V. scoparium* played negligible roles in the community structure compared to their roles in the granitic and quartzitic plant communities.

The forb component of the vegetation was a significant part of the limestone plant community, particularly in species diversity. Only two of the 51 forb species found in the study area were absent from limestone soils. In comparison, 37 forbs were found on quartzite and only 20 on granite. The forbs occupied almost one-third of the relative coverage on limestone. The principal forbs were in order of decreasing abundance:

Arnica latifolia, Aster conspicuus, Thalictrum occidentale, Arnica cordifolia, and *Antennaria racemosa.*

The graminoids covered over one-fourth of the limestone plots with *Calamagrostis rubescens* composing over 90 percent of this fraction (Figure 2).

The habitat types on limestone were generally the driest in the study area. These

TABLE 2. Relative canopy coverage of important species, including t-statistic, by substrate in the Garnet Mountains, Montana.

Species	Relative Coverage (percent)			t-test significance (95 percent level)		
	Limestone	Granite	Quartzite	L - G[+]	L-Q	G - Q
Pseudotsuga menziesii	34	12	21	*	*	*
Pinus contorta	0	18	8	*	*	*
Abies lasiocarpa	0	8	3	*	*	
TOTAL TREES (6)	34	42	33			
Arctostaphylos uva-ursi	—	4	1	*	*	*
Berberis repens	2	0	1	*		
Linnaea borealis	1	8	1	*		*
Symphoricarpos albus	2	—	1	*		
Vaccinium globulare	1	9	16	*	*	
Vaccinium scoparium	—	14	6	*	*	*
TOTAL SHRUBS (22)	7	39	27			
Antennaria racemosa	4	0	1	*		
Arnica cordifolia	4	1	1	*		
Arnica latifolia	7	3	6			
Aster conspicuus	6	0	1			
Thalictrum occidentale	4	0	1	*	*	
Xerophyllum tenax	0	9	9	*	*	
TOTAL FORBS (51)	33	15	25			
Calamagrostis rubescens	23	2	14	*		*
Carex geyeri	2	1	0			
TOTAL GRAMINOIDS (6)	25	3	15			
GRAND TOTAL (85)	99	99	100			

[+]L = Limestone, G = Granite, Q = Quartzite

TABLE 3. Relative coverage and species diversity according to life form on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

Substrate	Life Form				
	Trees	Shrubs	Forbs	Graminoids	TOTAL
LIMESTONE					
Relative coverage (percent)	34	7	33	25	99
Number of species	3	13	49	6	81
GRANITE					
Relative coverage (percent)	42	39	15	3	99
Number of species	5	14	20	4	43
QUARTZITE					
Relative coverage (percent)	33	27	25	15	100
Number of species	6	16	37	4	63

were principally *Pseudotsuga menziesii/Calamagrostis rubescens* with some plots classified as *P. menziesii/Symphoricarpos albus* and one as *P. menziesii/Carex geyeri.*

Granite: The vegetation on granite was composed of species characteristics of more mesic sites. The most prominent tree species was *Pinus contorta,* although *Pseudotsuga menziesii* and *Abies lasiocarpa* were also important. Of the three substrates, granite had the greatest relative tree coverage (42 percent).

The shrubs accounted for 39 percent relative coverage. The principal ones were *Vaccinium scoparium* and *V. globulare. Linnaea borealis* was also a dominant subshrub.

The forbs and graminoids played a minor role in the floristic composition on granitic soils. Together, they constituted about one-fourth of the relative coverage. *Xerophyllum tenax* and *Calamagrostis rubescens* were the prominent nonwoody plants.

The total amount of coverage was greater on granite than either quartzite or limestone (Goldin, 1976). The habitat types were in the *Abies lasiocarpa* series or the colder part of the *Pseudotsuga menziesii* series(*P. menziesii/Xerophyllum tenax).*

Quartzite: Coverage of each life form on quartzite was intermediate between the values on granite and limestone. *Pseudotsuga menziesii* and *Pinus contorta* were the dominant trees, and *Vaccinium globulare* and *V. scoparium* were the principal shrubs.

Forbs produced a relative coverage of 25 percent and graminoids 15 percent. *Xerophyllum tenax, Arnica latifolia,* and *Calamagrostis rubenscens* were the dominant plants in these groups.

Seven of the eight habitat types found in the study area were present on quartzite.

Ordination of stands: The Index-of-Similarity ordination indicated marked differences between limestone and granite. Limestone stands were clustered and isolated in the apparently dry section of the ordination while granite was associated with a similar pattern on the moist sites. The stands on these substrates were widely separated. The quartzite stands, on the other hand, were distributed throughout the ordination, but skewed toward the moist end (Figures 3 and 4).

The clustering indicates a relative homogeneity in stand structure on limestone and granite which was entirely absent on quartzite, probably as a result of the greater variability in the soil or quartzite parent rock. The distribution of habitat types also shows a general clustering.

The general sequence of prominent species from the dry limestone sites to the moist granitic sites based on abundance was the following: *Aster conspicuus, Calamagrostis rubescens, Thalictrum occidentale, Linnaea borealis, Arctostaphylos uva-ursi, Xerophyllum tenax, Vaccinium globulare, Pinus contorta, Vaccinium scoparium,* and *Abies lasiocarpa. Pseudotsuga menziesii, Antennaria racemosa,* and *Arnica latifolia* seemed to be

TABLE 4. Habitat type distribution on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

Habitat Type (Pfister *et al.*, 1974)	Limestone	Granite	Quartzite
Pseudotsuga menziesii/Carex geyeri	1		
P. menziesii/Calamagrostis rubescens	11		3
P. menziesii/Symphoricarpos albus	3		1
P. menziesii/Vaccinium globulare			1
P. menziesii/Xerophyllum tenax		2	3
Abies lasiocarpa/Linnaea borealis		9	2
A. lasiocarpa/Xerophyllum tenax		3	3
A. lasiocarpa/Menziesia ferruginea		1	2

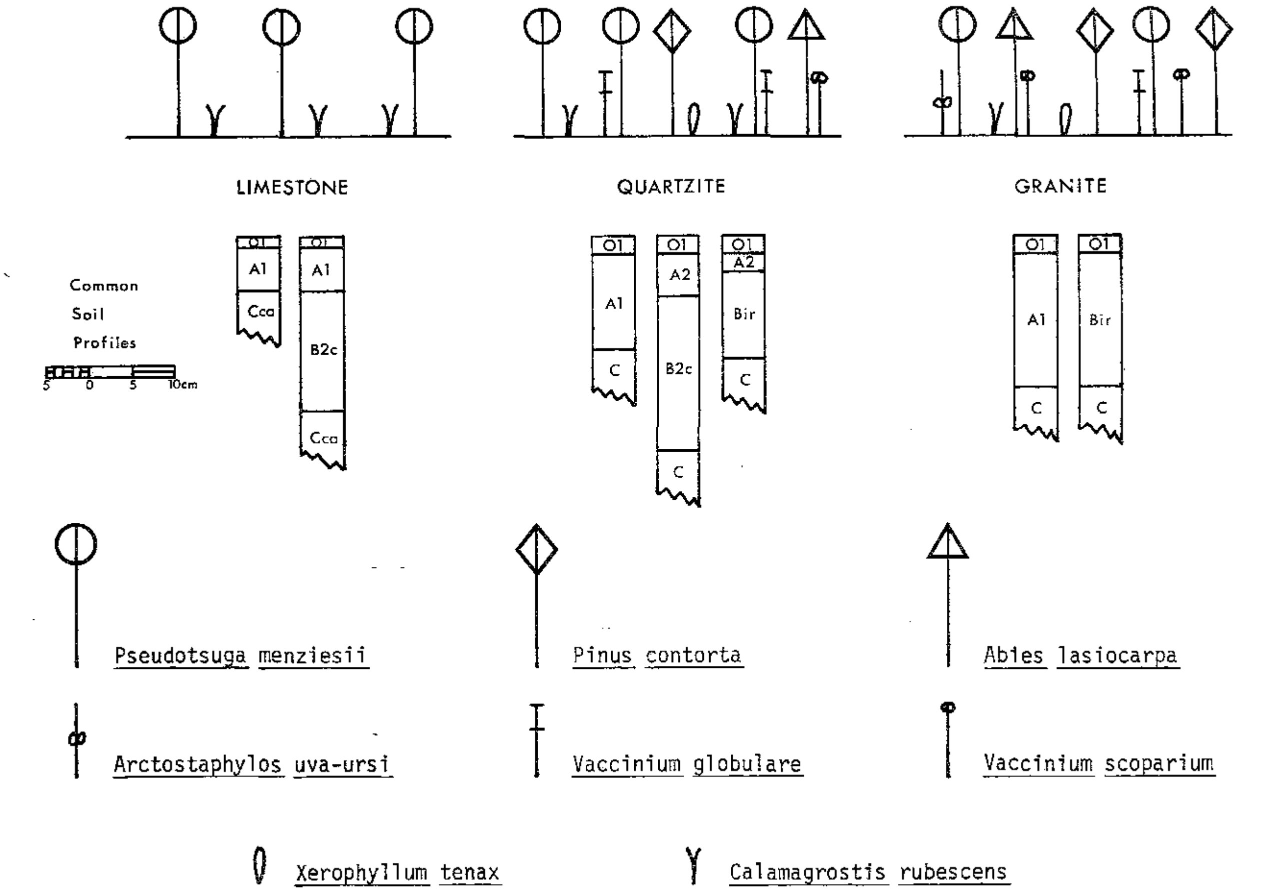

Figure 2. Vegetation patterns and common soil profiles on limestone, quartzite, and granite in the Garnet Mountains, Montana.

fairly well-distributed on all sites. Most of the differences in species distribution probably resulted from parent material differences; some effect may have been caused by minor random differences in the stage of plant succession (Goldin, 1976).

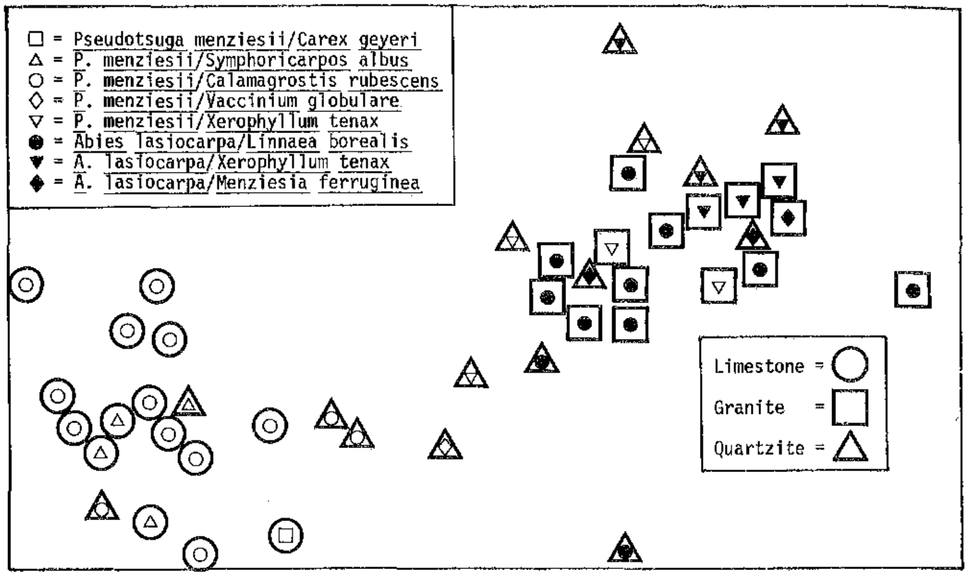

Figure 3. Ordination of stands on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana.

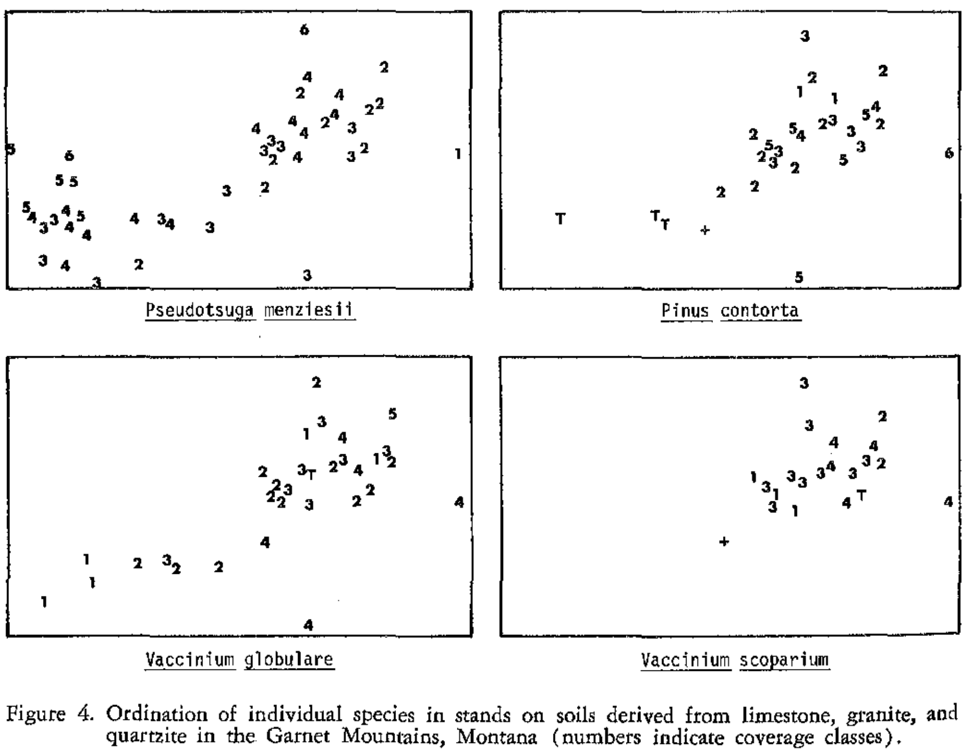

Figure 4. Ordination of individual species in stands on soils derived from limestone, granite, and quartzite in the Garnet Mountains, Montana (numbers indicate coverage classes).

Discussion

This study shows that definite differences occur in plant distribution and community structure according to the underlying substrate. While a detailed examination of soil moisture was not a part of this research, it appears that the distribution of plant species can be explained, at least in part, from the variations in this factor.

The unpublished theory of Herbert Holdorf (1976) for plant distribution on soils underlain by limestone bedrock in the Little Belt Mountains of Montana is based on observations of soil moisture effects resulting from differences in rock permeability. According to Holdorf, fractures in most limestone bedrock provide more continuous channels for water percolation than are found in either granite or quartzite, which are much more impermeable. Therefore, gravitational water remains longer in soils formed in the latter rocks, thereby delaying the period of drought. On limestone soils, water depletion begins immediately after snowmelt. Holdorf therefore considers limestone soils drier than soils formed in the other rocks, which results in a distinctive and more xeric plant community.

Pinus contorta has been found to occur on limestone soils where soil moisture is augmented by higher precipitation or impeded drainage (Goldin, 1976). This species has also been associated with calcareous glacial materials in Montana where drainage is impeded by impermeable rocks underlying the glacial debris (Holdorf, 1976). However, moisture itself may not be the only factor limiting its distribution, since this species can occur on both very wet and very dry sites. For shallow-rooted plants, such as the *Vaccinium* species or tree seedlings, the surface pH may be the key factor to plant distribution (Holdorf, 1976).

Much of the above discussion concerning the key role of soil moisture in plant distribution on limestone soils is speculative. This influence, however, is probably significant enough to warrant research on the soil moisture regime on soils underlain by limestone relative to those formed in acid materials.

Summary

On limestone and quartzite the dominant tree species was *Pseudotsuga menziesii;* on granite that position was held by *Pinus contorta. Pinus contorta* and *Abies lasiocarpa* rarely occurred on limestone. In the few areas where these species were found on limestone, some soil or topographic feature was present which probably resulted in an augmented moisture content. Thus, the data from this study and observations by field soil scientists suggest that the causative factor for the distribution of *Pinus contorta* and *Abies lasiocarpa* relates to the soil moisture regime.

Shrubs, particularly *Vaccinium globulare* and *V. scoparium,* provided negligible coverage in the plant communities over limestone bedrock, although they were abundant on the other substrates. The dominant shrubs on limestone *(Berberis repens* and *Symphoricarpos albus)* were absent or nearly so on granite and quartzite.

The dominant forb on granite and quartzite was *Xerophyllum tenax* and on limestone, *Arnica latifolia.* The former was rarely present on limestone; the latter occurred on all substrates.

Calamagrostis rubescens was the principal graminoid on all three substrates, although it was most prominent on limestone.

The greatest total species diversity occurred on limestone soils and the least on granite. Even though granite had only about half of the species diversity as limestone, it had greater total coverage than either limestone or quartzite. The coverage of each life form was very different, however. Granite was highest in tree and shrub coverage and lowest in forb and graminoid coverage. Limestone was highest in forb and graminoid coverage, lowest in shrub coverage, and high in tree coverage. Quartzite was intermediate in coverage values among all life forms.

Classification of the vegetation on each substrate by habitat types revealed marked differences, with limestone supporting the driest habitat types, granite the moistest, and quartzite the entire range.

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