

## Gradient analysis of forests of the Sangre de Cristo Range, Colorado

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Interrelationships between dominant compositional and environmental gradients were studied using 186 forest stands sampled on the east slope of the Sangre de Cristo Range, Colorado. Detrended correspondence analysis and detrended canonical correspondence analysis were used to analyze indirect and direct gradients, respectively. The dominant compositional gradient was strongly correlated with elevation. Increasing elevation was associated with decreasing soil pH and percent base saturation, and increasing total soil N. Ordination of stands stratified by elevation showed the major compositional gradient within each elevation class was strongly correlated with a topographic moisture index. Most soil variables correlated with this gradient in low and high elevation classes. In mid-elevation forests, a third compositional gradient correlated with soil pH, percent base saturation, and potential solar radiation. In these forests, *Pinus contorta* and *Pseudotsuga menziesii* were associated with acidic soils on north-facing slopes, whereas *Populus tremuloides* and *Abies concolor* were associated with base-rich soils on south-facing slopes. Ordination axes accounted for least variation in comparatively young mid-elevation forests. A plausible explanation is that the mid-elevation forests represent an unpredictable stage in forest development where competition has not yet had sufficient time to sort species along environmental gradients.

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Les interrelations entre les gradients de composition dominante et de l'environnement ont été étudiées dans 186 peuplements forestiers du versant est de la chaîne de Sangre de Cristo au Colorado. L'analyse détendancée des correspondances et l'analyse détendancée canonique des correspondances ont été utilisées pour examiner les gradients indirects et directs, respectivement. Le gradient de composition dominante a été fortement corrélé avec altitude. L'accroissement de l'altitude a été associé au pH décroissant du sol, au pourcentage de saturation en bases et à la teneur croissante en azote total du sol. L'ordination des peuplements stratifiés par l'altitude a montré que le principal gradient de composition de chaque classe d'altitude a été fortement corrélé avec ce gradient dans les classes de basse et de haute altitude. Dans les forêts de moyenne altitude, un troisième gradient a été corrélé avec le pH du sol, le pourcentage de saturation en bases et la radiation solaire potentielle. Dans ces forêts, *Pinus contorta* et *Pseudotsuga menziesii* ont été associés, sur les pentes exposées au nord, avec des sols acides alors que *Populus tremuloides* et *Abies concolor* ont été associées, sur les pentes exposées au sud, avec des sols riches en bases. Les axes d'ordination ont expliqué moins de variation dans les forêts relativement jeunes de moyenne altitude. Une explication plausible de ce fait serait que les forêts de moyenne altitude représentent un stade imprévisible de développement où la compétition n'a pas encore eu suffisamment de temps de trier les espèces le long d'un gradient environnemental.

[Traduit par la revue]

### Introduction

Variation in species composition and structure of montane forests is often interpreted in the context of complex gradients of elevation, topographic position, and post-disturbance development (e.g., Whittaker 1967; Peet 1981; Gagnon and Bradfield 1987). Increases in elevation are generally associated with decreases in temperature and evapotranspiration, and increases in precipitation and snow depth (Barry 1981; Henning and Henning 1981). For mountainous regions with low rainfall, such as the Southern Rocky Mountains, the relationship between vegetation and topographic position has usually been attributed to differences in site moisture status and evapotranspiration (e.g., Daubenmire 1943; Running and Nemani 1985; Peet 1988). In contrast, vegetation in high rainfall regions often varies with topographic position because geomorphic features are correlated with soil chemical and physical properties (e.g., Gagnon and Bradfield 1987; Reif and Allen 1988; McLeod 1988). Because elevation is positively correlated with site moisture status, species composition may be less influenced by moisture and more influenced by soil properties with increasing elevation in Southern Rocky Mountain forests. Soil

texture and chemistry have been thought to contribute to understory compositional variation in Rocky Mountain forests (e.g., Daubenmire 1943; DeVelice et al. 1986; Peet 1988). However, few studies have quantitatively related soil chemical and physical properties to compositional gradients (Smith 1985; Peet 1988). Frequency of disturbance events and rates of subsequent recovery also vary along dominant gradients (e.g., Peet 1981; Harmon et al. 1984). For example, Romme and Knight (1981) showed that in the Medicine Bow Mountains, fire is less frequent and succession more rapid in sheltered ravines and valley bottoms than in adjacent forests on uplands. Rarely have all these dominant gradients, and their interactions, been quantitatively examined for a particular locality.

The Sangre de Cristo Range forms the southeastern extension of the Southern Rocky Mountain massif. Forests of this range are floristically distinctive and can be rich in tree species relative to other Southern Rocky Mountain forests (Peet 1988). This study relates dominant compositional gradients in forests at one locality in the Sangre de Cristo Range to variation in site variables and stand age, and presents the results as gradient representations.<sup>2</sup> Gradient interrelationships are examined to

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<sup>2</sup>Botanical nomenclature follows Kartesz and Kartesz (1980) unless otherwise indicated.

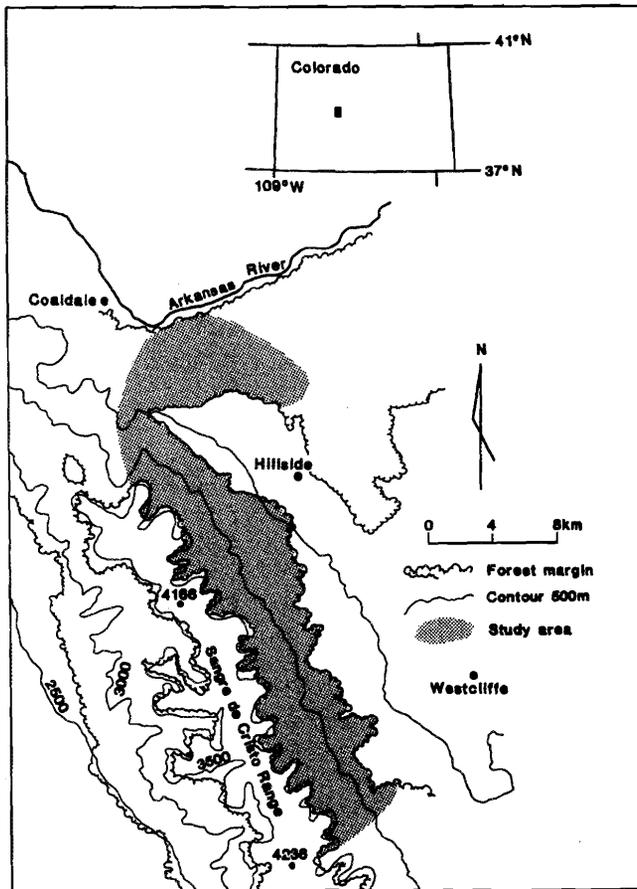


FIG. 1. Map showing location of the study area.

determine (i) whether the relative importance of and relationship between the topographic moisture gradient and a soil chemistry gradient depends on elevation; (ii) whether recent disturbance history relates to landscape position; and (iii) whether there are site differences between tree species found in mid-elevation forests rich in tree species.

### Study area

The study area is located on the eastern slope of the Sangre de Cristo Range (Fig. 1). In this region mountains rise to ca. 4250 m elevation, and forest occupies a broad elevational band between 2000 m and 3650 m elevation. The subalpine and montane forests of the study area (>2750 m elevation) are predominantly underlain by Pennsylvanian-Permian arkosic sandstones, siltstones, and conglomerates (U.S. Geological Survey 1979). Extensive Pleistocene glaciation occurred in these mountains and their physiography is partly the result of fluvial modification of formerly glaciated slopes. The interfluvial on lower slopes (<2750 m elevation) are a Tertiary sandstone, siltstone, and conglomerate complex. On slopes below 2250 m elevation, continuing down to the Arkansas river (Fig. 1), metamorphic felsic and hornblend gneisses occur with granitic intrusions (U.S. Geological Survey 1979).

Soil patterns in the mountainous areas of Colorado are complex with rapid changes over short distances (Johnson and Cline 1965; Smith 1985). Soils are typically young and coarse-textured with rocky fractions incorporated in the regolith. However, at higher elevations soils show greater profile and weathering (Johnson and Cline 1965; Carleton et al. 1974). Geomorphic processes are important in determining the distribution and pattern of soil types (Reider 1983). For example, along exposed ridge crests soils are often skeletal, contrast-

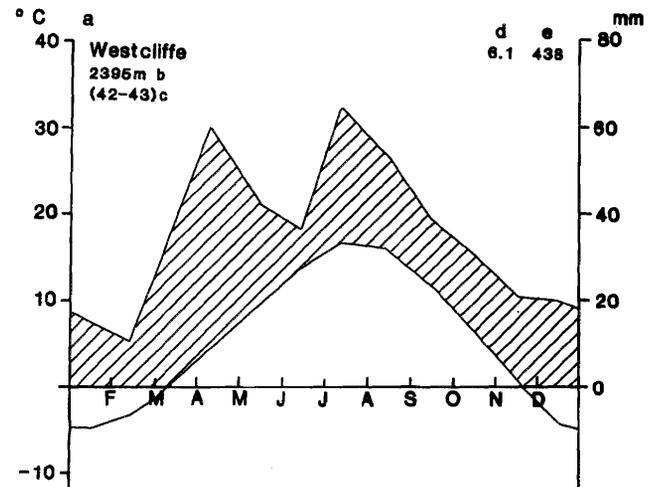


FIG. 2. Climate diagram (after Walter and Leith 1967) for the nearest climate station to study area. Abscissa is in months starting with January; each division on the ordinate is 10°C or 20 mm precipitation. a, station; b, elevation; c, number of years of records; d, mean annual temperature; e, mean annual precipitation.

ing with lower slopes and valley bottoms where alluvial and colluvial deposition often produce deep soils.

Only broad climatic patterns of the Sangre de Cristo Mountains have been described. Mean annual precipitation increases linearly with altitude, ranging from ca. 340 mm at 2135 m to 870 mm at 3650 m elevation (Baker 1944; Johnson and Cline 1965). Moist Gulf air brings precipitation to the eastern slopes during the spring and sometimes in the fall (Johnson and Cline 1965). Convective thunderstorms are responsible for most summer precipitation. Along a climatic transect up the east slope of the Front Range approximately 150 km north of the study area, mean annual temperature ranges from 8.3°C at 2195 m elevation to 3.3°C at 3750 m, for a lapse rate of 7.5°C per 1000 m (Barry 1973). The nearest climate station to the study area is located at Westcliffe, 8 km to the southeast at 2395 m elevation (Fig. 1). Figure 2 shows a climate diagram (after Walter and Leith 1967) for this station.

Anthropogenic influences on Southern Rocky Mountain forests have been both direct and indirect. Historically, fire has been the most important cultural impact. It is likely that the activity of early aboriginal people resulted in an increase in fire frequency, at least at low elevations (Peet 1988). The arrival of prospectors and farmers in the middle part of the nineteenth century led to a large increase in fire frequency. Extensive, destructive forest fires occurred between 1860 and 1890 in the Southern Rocky Mountains (Veblen and Lorenz 1986; Peet 1988), and the study area appears to have been no exception (Weber 1976; Athearn 1985). These forests take several hundred years, at least, to recover from such fires (Peet 1988).

### Methods

#### Data collection

Potential sample sites were classified into seven elevation and five topographic position classes. Plots were located subjectively to cover the range of possible combinations of elevation, topographic position, and stand age as suggested by Peet (1981), Austin (1985), and Knox (1987). Only comparatively homogeneous forest stands were included (Mueller-Dombois and Ellenberg 1974). A total of 186 0.1-ha plots were sampled (Table 1).

Each sample was a 50 × 20 m (0.1 ha) plot. A list was compiled of all vascular plant species rooted within the plot. Each species was assigned a cover-abundance score, similar to that of Braun-Blanquet (Mueller-Dombois and Ellenberg 1974), using an eight-class scale (7, >75% cover; 6, 51-75%; 5, 26-50%; 4, 6-25%; 3, 3-5%; 2, 1-2%; 1, a few plants, <1%; 0, solitary, with small cover).

TABLE 1. Distribution of 186 plots within seven elevational classes and five topographic position classes

Elevation (m)	Topographic position				
	Valley bottom	Concave slope	Mid-slope	Convex slope	Ridge crest
>3300	4	4	7	6	7
3100-3300	2	9	10	4	3
2900-3100	3	6	9	5	4
2700-2900	6	3	9	10	6
2500-2700	3	4	5	4	3
2300-2500	3	3	6	4	3
<2300	6	6	8	5	6

All trees >2 cm diameter at breast height were recorded by species and diameter. In addition, usually two or more of what appeared to be the oldest trees (usually the largest) of each canopy species were cored so that maximum tree age could be used as an index of stand age. Cores were taken as near as possible to the ground (generally <10 cm).

Within each plot site information was collected for a typical point near the plot center. Elevation, aspect, and slope were recorded. Subjective five-point indices were recorded for topographic position ranging from valley bottom through concave and convex slopes to ridges or hilltops, and for exposure ranging from sheltered to open hillside or exposed ridge top. Soil was collected at six locations along the 50 m center line of the plot and composited. Soil samples were taken from the top 10 cm below the litter layer.

Subsamples of each soil composite were analyzed using the methods of the North Carolina Soil Testing Laboratory, Raleigh, NC. Percent humic matter (humic and fulvic material), pH, cation exchange capacity (CEC; mequiv./100 g), % base saturation, available (extractable) P (mg/kg), and extractable cations (Ca, Mg, K; mequiv./100 g) were determined. The extract used was 0.25 M  $\text{NH}_4\text{NO}_3$  - 0.15 M  $\text{NH}_4\text{F}$  - 0.2 M  $\text{CH}_3\text{COOH}$  - 0.13 M  $\text{HNO}_3$  - 0.001 M EDTA buffered at pH 2.5. Soil texture was determined on subsamples of the composites using a modification of the Bouyoucos hydrometer method (Patrick 1958). Total (Kjeldahl) N (mg/kg) was determined for a finely ground subsample from each composite using a Technicon Auto-Analyzer and aluminium block digester (Isaac and Johnson 1976).

#### Data analysis

Potential solar radiation, topographic position, and exposure strongly influence soil moisture regimes through water runoff and evapotranspiration (e.g., Jenny 1980; Birkland 1984; Lieffers and Larkin-Lieffers 1987). These components of the complex soil moisture gradient can be combined to construct subjective indices of relative site moisture status (e.g., Whittaker 1967; Wentworth 1981; Peet 1981). A topographic moisture index was constructed for the present study using the following expression:

$$\text{topographic moisture index} = 8 - \left( \frac{\text{topographic position index} + \text{exposure index}}{2} + \text{solar radiation index} \right)$$

Potential solar radiation was interpolated from the tables of Frank and Lee (1966) and relativized linearly to the potential solar radiation index with a scale of 0 to 2. Because of a fivefold range in the average of the topographic position and exposure indices, the topographic moisture index was more sensitive to topographic position and exposure than potential solar radiation. Field experience supported these relative contributions to the topographic moisture index.

Compositional gradients, and their relationships to sixteen environmental variables (see Fig. 3) were investigated by detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA), using the computer program CANOCO (Version 2.1; ter Braak 1987a). DCA extracts the dominant compositional gradients

from a species by site data matrix, irrespective of site variables, whereas DCCA extracts the dominant gradients given the constraint that they must be orthogonal linear combinations of supplied environmental variables (ter Braak 1987a). The eigenvalues in DCA and DCCA indicate the amount of variation accounted for by an axis, whereas gradient length represents the amount of species turnover along an axis (ter Braak 1987a). A comparison of DCCA and DCA eigenvalues thus indicates the importance of compositional gradients not accounted for by measured site variables. DCCA has interpretive advantages over conventional floristic ordination (DCA; Cramer and Hytteborn 1987; ter Braak 1987a, 1987b). Because ordination results are rarely interpretable beyond two or three dimensions (Peet 1980; Knox 1987), the data set was stratified by elevation to reduce the importance of the elevation gradient for some analyses (see Peet 1980). Such stratification can overcome the complex, nonlinear interactions of site variables. Ordinations were run using the default options in the CANOCO algorithm, with detrending by segments. Raw cover abundance scores (0-7) were used in the analysis, except that a score of 0 was given the value 0.1.

Minimum stand age (defined as the oldest dominant tree aged from a stand) was used as an indicator of stand age (see Romme and Knight 1981). The stand age estimated in this study reflects the time since catastrophic disturbance, usually stand-destroying fires. This relationship is more tenuous in older forest.

## Results

### Gradient structure

DCCA eigenvalues were usually only marginally lower than the DCA eigenvalues, thus indicating that the two ordination methods accounted for similar variation (Table 2). This is consistent with the similar gradient lengths generated by the two methods (Table 2).

Spearman's rank correlations (using SAS Institute Inc. 1985a) showed that both for the data set as a whole and within each elevation class, first axis DCA and DCCA ordination stand scores were similar (Table 2). Rank correlations of DCA and DCCA stand scores for the second axis showed that these floristic gradients were similar for six of seven elevation strata. Overall, the two ordination methods gave similar solutions with DCCA having the advantage of providing a direct gradient representation.

DCA and DCCA eigenvalues and gradient lengths varied with elevation (Table 2). First axis eigenvalues decreased with increasing elevation until near timberline where there was a slight increase. Similarly, first axis gradient lengths declined with increasing elevation until near timberline, where they increased again. Second axes eigenvalues and gradient lengths were lowest near the center of the elevational range and increased towards the elevational limits of the forest.

### Compositional and environmental gradients

Stand scores and environmental vectors for a DCCA ordination of all 186 stands and 510 taxa are shown in Fig. 3a. The vectors point in the direction of maximum change of the specified site variables, and vector lengths indicate the degree of correlation between variables and axes (ter Braak 1987b). The first DCCA axis was correlated most strongly with elevation and was negatively correlated with soil pH and percent base saturation. The second DCCA axis was correlated most strongly with the topographic moisture index, with the moisture index vector virtually orthogonal to the elevation vector (Fig. 3a). Cation exchange capacity (CEC), Ca, and Mg increased along the second axis. Total N increased with both elevation and the topographic moisture index.

TABLE 2. Eigenvalues and gradient lengths (SD) for first and second axes of DCA and DCCA ordinations for the data set divided into seven elevation classes and the total data set

Elevation (m)	Axis	Eigenvalues		Gradient length		$r_s$
		DCA	DCCA	DCA	DCCA	
>3300	1	0.576	0.568	3.704	3.719	0.99***
	2	0.291	0.310	2.741	2.644	0.99***
3100-3300	1	0.459	0.448	2.847	2.754	0.99***
	2	0.235	0.214	2.186	2.250	0.93***
2900-3100	1	0.457	0.443	3.001	2.870	0.99***
	2	0.175	0.199	1.723	1.978	0.63***
2700-2900	1	0.543	0.486	3.755	3.611	0.99***
	2	0.158	0.198	2.089	2.122	0.44**
2500-2700	1	0.661	0.660	4.305	4.174	0.99***
	2	0.211	0.213	2.374	1.913	0.71***
2300-2500	1	0.737	0.730	4.198	4.532	0.99***
	2	0.302	0.297	2.576	2.678	0.89***
<2300	1	0.721	0.694	5.011	5.136	0.99***
	2	0.220	0.189	2.010	2.052	0.08
Total	1	0.760	0.175	7.436	7.848	0.99***
	2	0.362	0.313	3.588	3.385	0.90***

NOTE: Also given are Spearman's rank correlations ( $r_s$ ) of first and second DCA axes stand scores with first and second DCCA axes stand scores. \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.01$ .

Ordination of stands stratified by elevation showed that the first DCCA axis, within each elevation class, was most strongly correlated with the topographic moisture index. What changed between elevation classes was the interrelationships between site variables and stand age (Figs. 3b to 3h), as well as the positions and combinations of canopy tree species found along dominant gradients (Table 3).

The DCCA ordination of stands above 3300 m elevation showed that most soil chemistry variables strongly correlated with the first axis (Fig. 3b). The second axis was most strongly correlated with increasing available P and decreasing elevation. This may be because the forest was sampled to higher elevation on upslope positions, as forests were absent from the valley bottom at such elevations. Low first and second axis species scores indicated *Pinus aristata* dominated the highest and driest forests (Table 3).

The first DCCA axis from ordination of stands between 3100 and 3300 m elevation negatively correlated with percent base saturation, pH, and potential solar radiation (Fig. 3c). Total N increased along the first axis. *Pinus flexilis* and *P. aristata* dominated the drier sites, with *Abies lasiocarpa* and *Picea engelmannii* widely distributed (Table 3). The second axis appeared weakly correlated with increasing pH, % sand, potential solar radiation, and percent base saturation, and decreasing minimum stand age. Low second axis species scores for *Pinus flexilis* and *Abies lasiocarpa* indicate they were found in older forest on northerly slopes with acid soils (Table 3).

The DCCA ordination of stands between 2900 and 3100 m elevation showed environmental vectors (Fig. 3d) had a similar pattern to those of the previous elevation class. Soil cations appeared to be less strongly related to the first axis than at higher elevations. *Pinus flexilis* was a common species on dry sites, with *Abies lasiocarpa* and *Picea engelmannii* on moist sites (Table 3).

Stands sampled between 2700 and 2900 m elevation were often rich in tree species (Table 3). The first DCCA axis correlated strongly with decreasing potential solar radiation and percent humic matter (Fig. 3e). Moist sites may have low percent humic matter because streams were actively degrading in this elevational class. *Pinus ponderosa* was found at the dry end of the first axis, whereas *Abies lasiocarpa* and *Picea engelmannii* had species scores at the moist end (Table 3).

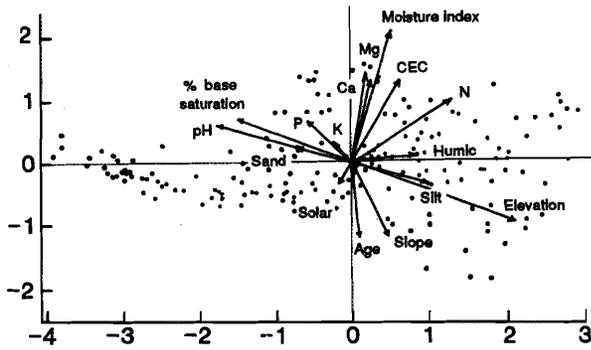
Soil pH, percent sand, and percent base saturation increased along the second axis. These vectors are nearly orthogonal to the moisture index and distinguish acidic, coarse-textured soils on north-facing slopes from base-rich soils on south-facing slopes. In this elevation class several soil characteristics clearly determine a second axis rather than correlate with the moisture index. Second-axis species scores were ordered *Pinus contorta*, *Pseudotsuga menziesii*, *Populus tremuloides*, *Abies concolor*, and *Picea engelmannii* (Table 3).

Species scores from a DCCA ordination of stands between 2500 and 2700 m elevation indicate that *Pinus edulis* was restricted to dry sites, whereas species characteristic of high elevations such as *Populus tremuloides* and *Picea engelmannii* were found only on moist sites (Table 3). CEC, total N, and cations (Ca, Mg) increased along both the first and second axes (Fig. 3f). The second axis strongly correlated with increasing potential solar radiation, soil pH, and percent base saturation. The grouping of these three site variables indicates that slope orientation relates to soil development in mid-elevation forests (see Figs. 3c to 3f). Dominant tree species along the second axis, listed with increasing species scores, included *Pinus flexilis*, *P. ponderosa*, *Pseudotsuga menziesii*, *Populus tremuloides*, and *Abies concolor* (Table 3).

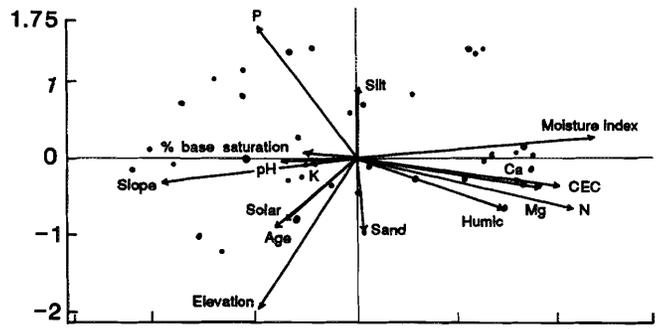
Ordination of stands between 2300 and 2500 m elevation resulted in a maximum direction of change for the topographic moisture index that nearly paralleled the first DCCA axis (Fig. 3g). Soil CEC, extractable cations (Ca, Mg), and total N

FIG. 3. Stand scores (●) for first and second axes of a DCCA ordination of all 186 forest stands, as well as ordinations of stands divided into seven elevation strata. Vectors indicate the direction of maximum change for a site variable and length indicates the strength of their correlation with the ordination axes.

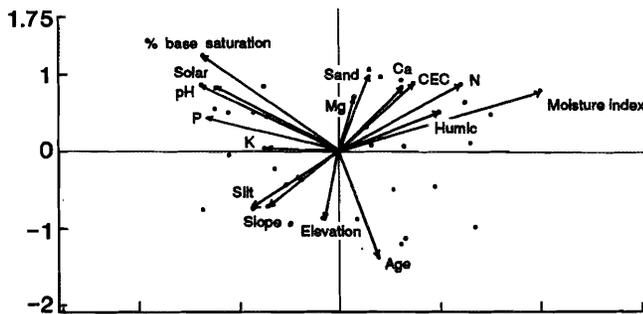
(a) All Plots



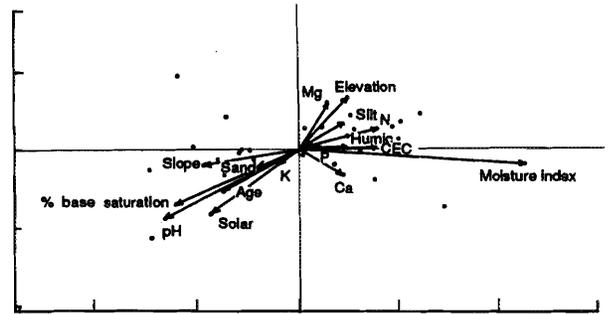
(b) > 3300m Elevation



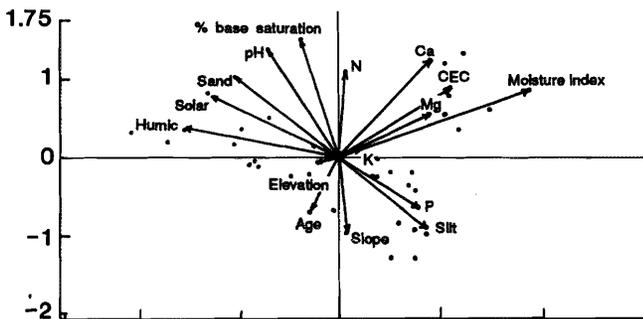
(c) 3100-3300m Elevation



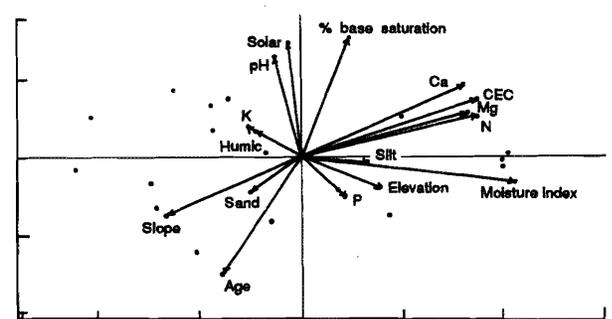
(d) 2900-3100m Elevation



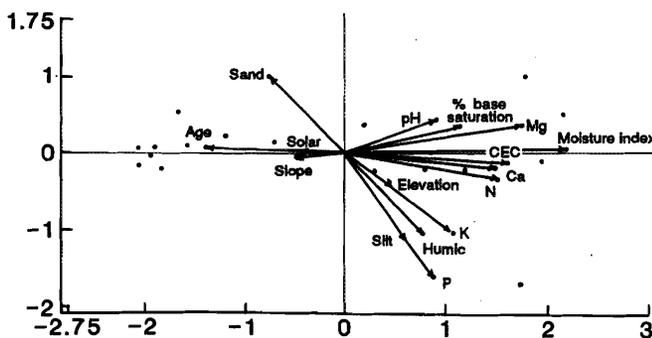
(e) 2700-2900m Elevation



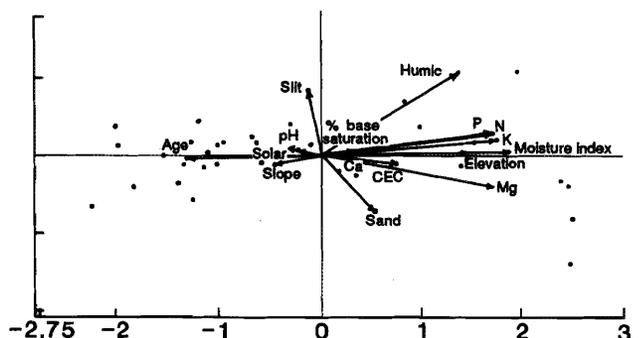
(f) 2500-2700m Elevation



(g) 2300-2500m Elevation



(h) < 2300m Elevation



AXIS 2

AXIS 1

TABLE 3. First and second DCCA axes tree species scores for the total

Species	Total		<2300 m		2300–2500 m	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
<i>Abies concolor</i>	-0.57	1.01	2.75	-1.31	1.79	-1.25
<i>Abies lasiocarpa</i>	2.38	0.17				
<i>Alnus tenuifolia</i> Nutt.	-0.60	2.66	(3.46)	(-1.56)	(2.73)	(1.69)
<i>Betula occidentalis</i>	-1.07	2.56	(3.01)	(-2.41)	(2.72)	(-1.94)
<i>Juniperus monosperma</i>	-4.13	0.62	-2.81	-1.39	(-2.38)	(-0.83)
<i>Juniperus scopulorum</i>	-2.27	0.77	0.87	-0.25	-0.29	0.57
<i>Picea engelmannii</i>	2.27	-0.75	(2.97)	(-0.92)	(2.26)	(2.45)
<i>Pinus aristata</i>	1.55	-2.18				
<i>Pinus contorta</i>	0.10	-0.56				
<i>Pinus edulis</i>	-3.45	0.00	-1.45	-0.08	-2.26	0.08
<i>Pinus flexilis</i>	0.63	-1.83				
<i>Pinus ponderosa</i>	-1.43	-0.94	0.66	-1.16	-0.26	0.27
<i>Populus angustifolia</i>	-0.77	2.72	3.21	-1.40	(1.20)	(3.22)
<i>Populus tremuloides</i>	0.49	0.57	(2.76)	(-1.09)	(-2.08)	1.54
<i>Pseudotsuga menziesii</i>	-0.86	0.92	2.21	-1.44	0.95	1.19

NOTE: Scores in parentheses indicate species found on less than 5% of the stands in an elevation class.

increased along the first axis. Most soil variables in the lower elevation classes showed maximum direction of change along the moisture gradient, as in the highest elevation class. Solar radiation appeared to be a more important variable in elevation classes above 2500 m than below (Fig. 3). Dominant tree species along the first axis were, from dry to moist, *Pinus edulis*, *Juniperus scopulorum*, *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Abies concolor* (Table 3). In the lower elevation ordinations, minimum stand age declined along the first axis compared with the first and second axes in higher elevation classes. This DCCA ordination distinguished a second gradient of variation, with available P declining along the second DCCA axis. *Abies concolor* had a low second axis species score (high P), while *Populus tremuloides* and *Pseudotsuga menziesii* had comparatively high second axis species scores (low P; Table 3).

The first DCCA axis from an ordination of stands below 2300 m elevation correlated with increasing soil cations (Mg, K), extractable P, total N, and percent humic matter (Fig. 3h). In dry environments, higher levels of soil cations on wetter sites result from downslope transportation and increased weathering rates (Birkland 1984). The correlation of elevation with the first axis may be an artifact of the distribution of riparian stands, which were encountered primarily near the upper limit of the elevation stratum. Tree species dominance shifted along the first axis, from *Juniperus monosperma* at the dry end, through *Pinus edulis* and *Pseudotsuga menziesii*, to *Populus angustifolia* (Table 3).

#### Stand age

The frequency distribution of minimum stand age in the study area indicated the influence of disturbance on vegetation patterns. The mean minimum stand age was 202.5 years, with 50% of the stands sampled being less than 140 years old. When minimum stand age was plotted as isolines against elevation and the topographic moisture index, using PROC GCONTOUR (SAS Institute Inc. 1985b), a clear relationship emerged (Fig. 4). Above 3200 m elevation, minimum stand age increased to timberline, particularly at the drier end of the moisture gradient. Most stands sampled in the mid-elevation

forests (2500–3200 m) were 100–150 years old. Forests at low elevations and on dry sites often included trees over 200 years old. On such sites the wide spacing of individual trees and low fuel loads appear to minimize the likelihood of catastrophic disturbance. In contrast, on low elevation moist sites, stands were usually 100–150 years old. Although minimum stand age probably reflected time since catastrophic fire in many of the younger stands, this relationship was more tenuous in older forest. Although the pattern shown in Fig. 4 was based on subjectively located stands, observations support this pattern as general for the study area.

#### Discussion

The species composition of forests in the Sangre de Cristo Mountains is primarily controlled by gradients of elevation and site moisture status (topographic moisture index) as has been reported in studies of other portions of the Southern Rocky Mountains (e.g., Peet 1981; Smith 1985; Peet 1988). In this study, increasing elevation was also associated with decreasing soil pH, percent base saturation, and increasing total N. These soil patterns appear general for mountain slopes where temperature decreases and rainfall increases with elevation (Whittaker et al. 1968; Carleton et al. 1974; Buol et al. 1980).

Ordination of stands in elevation classes showed that the interrelationship between compositional gradients, site moisture, soil variation, and stand age were complex. In mountainous regions soil variation is often closely linked with slope orientation, angle, and position (Jenny 1980; Birkland 1984). In low and high elevation classes, most soil variables were strongly correlated with the topographic moisture gradient. At high elevations, soil cations increased with moisture index, yet percent base saturation declined (Figs. 3b–3d). At low elevations soil cations increased strongly and percent base saturation increased weakly with moisture index (Figs. 3g and 3h). The relationships between soils and the topographically related moisture index found in this study are generally consistent with patterns from regions of more humid environments for high elevations and dry environments for low elevations (Ollier 1976; Birkland 1984).

data set and the data set divided into seven elevation classes

2500–2700 m		2700–2900 m		2900–3100 m		3100–3300 m		>3300 m	
Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
0.92 (2.94) (2.95)	0.68 (-0.87) (-0.19)	-0.08 2.00	0.39 -0.77	-1.11 1.61	0.28 -0.95	(-2.45) 0.89	(-0.57) -1.44	1.07	1.26
				(0.12)	(-1.57)				
-0.87 (2.94) (0.92) (1.08)	0.07 (-0.35) (1.70) (-1.88)	(-2.24) 1.75	(-0.40) 1.21	(-2.09) 1.29 (-0.25)	(-1.16) -1.33 (1.40)	0.41 -1.31	-0.97 -0.34	0.28 -1.49 (-0.99)	0.88 -0.21 (2.75)
-2.78 0.06 -0.71	0.46 -1.46 -1.22	(-3.27) -0.88 -1.46 (3.14)	(0.20) -0.11 0.38 (-0.03)	(-2.53) -1.43 (-2.23)	(3.07) -1.17 (1.90)	-1.45	-1.66	-1.95	2.35
2.09 0.27	-0.39 -0.76	0.74 0.31	-0.03 -0.63	0.10 0.51	-0.63 1.17	-1.15 (-1.05)	0.63 (-4.48)	-1.83	2.99

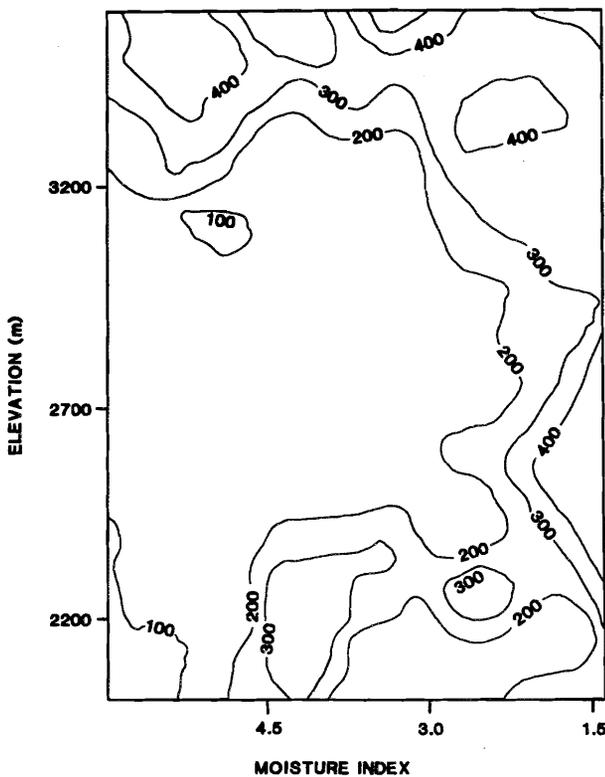


FIG. 4. Minimum stand age plotted against gradients of elevation and moisture. Contours indicate average time since catastrophic disturbance.

Composition of mid-elevational forests was also related to a third gradient that correlated with several soil characteristics and slope orientation. Such a pattern was only apparent after the data set had been stratified into elevation classes and supports the view that interpretive advantages result from stratifying complex data sets (Peet 1980). In these forests, *Pinus contorta* predominated on sites with acidic, infertile soils that were usually found on north-facing slopes. In contrast, *Populus tremuloides* dominated sites with comparatively base-rich

soils found on south-facing slopes. This soil-vegetation relationship has been described elsewhere (Hoff 1957; Langenheim 1962; Parker and Parker 1983). Dominance of *Pinus contorta* is commonly related to recent disturbance and acidic, infertile soils (e.g., Daubenmire 1943; Zinke 1962; Despain 1973; Whipple and Dix 1977; Peet 1988). Such soils are widespread farther north in the Rocky Mountains where *Pinus contorta* has a more extensive distribution (LaRoi and Hnatuik 1980; Peet 1981). Although *Abies concolor* and *Pseudotsuga menziesii* can codominate mid-elevation forests of the study area and to the south and west (Niering and Lowe 1984; DeVelice et al. 1986; Peet 1988), there were also site differences in the study area. *Pseudotsuga menziesii* was found on drier and less fertile sites than *Abies concolor*. Such examples suggest that latitudinal variation in species composition of mid-elevation forests correlates with variation in soil properties. A detailed and systematic investigation of compositional gradients at different latitudes supports this view (Allen 1988).

The distribution of stand ages with respect to elevation was largely consistent with that found in other Rocky Mountain forests where stand-destroying fires are common (Tande 1979; Arno 1980; Peet 1988). The extensive upper montane and lower subalpine forests with uniform minimum stand age commonly originated following stand replacing crown fires (Daubenmire 1943; Whipple and Dix 1977; LaRoi and Hnatuik 1980).

The results of this study do not support the notion that catastrophic disturbance is less frequent on moist sites. For any given elevation, the minimum stand age was comparatively low on moist sites (Figs. 3a and 4). This implies that forests on moist sites have been subjected to stand-destroying fires more frequently than upland sites. Romme and Knight (1981) concluded that for a subalpine forest in the Medicine Bow Mountains, fires were less frequent at the moist end of a topographic moisture gradient, a pattern described elsewhere in western United States (Arno 1980; Martin 1982). With increasing latitude there is a reduction in potential solar radiation, which may lead to lower flammability (sensu Knight 1987) for forests on moist sites in the subalpine zone. It appears the moist, cool end of the moisture gradient in the Medicine

Bow Mountains is absent from the gradient in the study area, with a concomitant extension at the dry end of the moisture gradient. The implication of this result is that there may be predictable patterns in disturbance regimes with changing latitude.

Eigenvalues from the elevation class ordinations showed that the amount of variation accounted for by the site variables changed with elevation (Table 2). The increasing first axes (moisture) eigenvalues, with decreasing elevation, may in part reflect an increase in control of species composition by moisture. This may be because potential evapotranspiration increases and precipitation decreases with decreasing elevation. However, this fails to explain the lower second axes eigenvalues in mid-elevation forests. These forests are comparatively young (Fig. 4), and some species have distributions reflecting recent disturbance (Allen 1988). A plausible explanation for the low eigenvalues in mid-elevation forests is that they represent a stage in forest development where competition has not yet had sufficient time to sort species along environmental gradients (see Christensen and Peet 1984).

Results of this study have implications for the most common form of forest classification in western United States, the habitat-type methodology (Daubenmire 1976; Alexander 1985). This methodology, which has been applied to the study area by DeVelice et al. (1986), is predicated on an understanding of forest development gradients and classifies vegetation according to potential natural communities. In fact, the development of such an understanding is severely restricted in the forests rich in mid-elevation tree species because of the limited range of stand ages present and the apparent unpredictability of species composition. Fire has been emphasized in most disturbance studies and used to explain the dominance of species such as *Pinus contorta* and *Populus tremuloides* (Peet 1988). It may be that without further disturbance, shade tolerants such as *Abies concolor* and *Pseudotsuga menziesii* will come to dominate most of the mid-elevation forest in the study area. However, the mechanisms for coexistence of many combinations of tree species found in the study area need further study.

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