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Plant communities associated with *Pinus ponderosa* forests in the sky islands of the Davis Mountains, Texas[1]

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Bataineh, M. M. (Department of Natural Resources and Environment, Jordan University of Science and Technology, P.O. Box 3030, Irbid, Jordan 22110), B. P. Oswald, A. L. Bataineh, K. W. Farrish, and D. W. Coble (Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, P.O. Box 6109, SFA Station, Nacogdoches, TX 75962), and C. B. Edminster (U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, AZ 86001). Plant communities associated with *Pinus ponderosa* forests in the sky islands of the Davis Mountains, Texas. J. Torrey Bot. Soc. 134: 468–478. 2007.—Species composition of *Pinus ponderosa* P.&C. Lawson var. *scopulorum* Engelm. forests in the sky islands of the Davis Mountains was evaluated and classified using ordination and classification techniques. Twelve study sites were established within *Pinus ponderosa* forests in the summers of 2002 and 2003. Overstory (tree) and understory (shrub and herbaceous) vegetation strata were sampled. Thirteen associations were recognized by combining four overstory groups and eight understory groups. The associations reflected a wide range of ecological conditions with *Juniperus deppeana* associations occupying dry sites and *Pinus ponderosa* associations occupying wetter sites. The major environmental factors responsible for the differences in vegetation of these forests were altitude, slope position, slope inclination, and soil moisture.

Key words: cluster analysis, indirect gradient analysis, *Juniper deppeana*, Madrean Archipelago, ordination, *Pinus cembroides*, Trans-Pecos.

The sky islands of the Davis Mountains, as well as other sky islands of the Madrean Archipelago, represent unique phenomena in ecosystem biodiversity and genetic variation. The isolation of these ecosystems by valleys and desert seas from other ecosystems is analogous to the isolation of oceanic islands by saltwater seas (Warshall 1995). These isolated ecosystems may be the least studied and most neglected of all ecosystems in North America (DeBano and Ffolliott 1995). Warshall (1995) attributed the Madrean Archipelago's unique biodiversity to its position as a "stepping stone" between the Rocky Mountains and the Sierra Madre Mountains, its configuration which allows for the convergence of northern and southern floristic and faunal realms, and the convergence of three climatic zones (tropical, subtropical, and temperate) in the Madrean Archipelago.

Sky islands vegetation, mainly those of the Santa Catalina Mountains and the Chiricahua Mountains, were the focus of several studies that aimed to list, describe, and compare plant communities along a variety of physiognomic and environmental gradients. Whittaker and Niering (1965) described and compared plant communities along an elevation gradient of the southwestern slopes of the Santa Catalina Mountains. Greater numbers of species and growth-form diversity were associated with xeric communities of the desert-grasslands and mountain-grasslands. In an earlier study, Whittaker and Niering (1964) examined the distribution of 700 species in relation to elevation and moisture gradients of the south slope. Species distributions along elevation

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and moisture gradients of the north slope of the Santa Catalina Mountains were also examined (Whittaker and Niering 1968). Barton (1994) used direct and indirect gradient analysis techniques to examine vegetation patterns along an elevation gradient in the Chiricahua Mountains.

Forests and woodlands of the Trans-Pecos Mountains, including the Davis Mountains, were classified to the series level (Diamond et al. 1987), where four series were identified: 1) *Pseudotsuga menziesii* (Mirbel) Franco var. *glauca* (Beissn.) Franco–*Pinus* spp. L.; 2) *Pinus ponderosa* P. & C. Lawson; 3) *Pinus cembroides* Zucc./*P. edulis* Engelm.–*Quercus* spp. L.–*Juniperus* spp. L.; and 4) *Quercus grisea* Liebm.–*Quercus* spp. Woodlands of the Guadalupe Mountains were classified to four (series equivalent) dominance types: 1) *Quercus grisea–Juniperus monosperma* (Engelm.) Sarg.; 2) *Quercus grisea–Juniperus deppeana* Steud.; 3) *Juniperus* spp.–*Pinus edulis*; and 4) *Juglans microcarpa* Berl.–*Dasylirion leiophyllum* Engelm. ex Trel. (Gehlbach 1967).

Although complete analysis of vegetation of the Davis Mountains is beyond the scope of this paper, quantitative description of local plant communities may provide an insight into vegetation patterns, at relatively small spatial scales, as well as serve as a baseline for future successional studies. In addition, an understanding of local variation in plant communities may aid in setting, guiding, and constraining management goals and activities. For example, restoration of *Pinus ponderosa* communities may benefit from the identification of variation patterns within these communities. Furthermore, examination of local vegetation patterns and the ordination of vegetation samples may aid in the recognition of major environmental gradients influencing the species distributions (Whittaker 1975). The objectives of this study were to describe and evaluate plant communities associated with *Pinus ponderosa* forests as well as attempt to relate variation patterns within these communities to major environmental gradients through the two-step approach of indirect gradient analysis.

Materials and Methods. Study Area. The study was conducted within The Nature Conservancy Davis Mountains Preserve, Jeff Davis County, Texas. Cool temperate climate characterizes the area. Average annual precipitation is approximately 60 cm (a 70-year mean of Mount Locke Station for the period 1935–2004). In 2003, total precipitation reached 60.7 cm (NOAA 2005). Summer monsoons comprise two-thirds of the annual rainfall (Turner 1977). Soils of the study area belong mainly to the Puerta-Madrone association. Loghouse association soils, however, occur near and along stream channels of the study area. The Puerta-Madrone association belongs to the Puerta soil series that is characterized by shallow, well-drained, noncalcareous, gravelly soils. The Loghouse association belongs to the Loghouse soil series that is characterized by deep, well-drained, gravelly soils (Turner 1977).

Sampling Design. In order to study plant communities associated with *Pinus ponderosa* forests, twelve study sites (each 4 ha in area) were established, eight in 2002 and four in 2003, subjectively but without preconceived bias (Muller-Dombois and Ellenberg 1974). Each site was divided into 16 plots (50×50 m) that were permanently marked and located using a Global Positioning System receiver (Garmin™ GPS). Ten plots within each site were randomly and independently chosen for sampling. A 20×50 m subplot was delineated within each plot using tapes where overstory (tree) and understory (woody seedlings, shrubs, and herbaceous) vegetation strata were sampled. Overstory and understory vegetation were identified to the species level when possible and higher taxa (genus) were used when identification at the species level was not possible. The USDA PLANTS database (http://plants.usda.gov) was used as the authority for the scientific names of plants and their authorities. Diameters at breast height (1.3 m) of all trees (height $\geq$ 1.4 m) were measured to the nearest 0.1 cm. Percent cover of understory vegetation was visually estimated using Daubenmire (1968) classes in ten 1 m^2 quadrats that were systematically nested within each 20×50 m subplot (Stohlgren et al. 1995). Altitude above sea level (m), slope inclination (%), aspect, and position on slope, where applicable, were determined for each plot (50×50 m). Mineral soil samples from the A-horizon were collected from three random locations within each plot to determine acidity or alkalinity (pH) and nutrient content in mg kg^{-1} (i.e., total N, P, K, Ca, Mg, S, and Na) of the A-horizon. Samples were tested at the Soil, Plant & Water Analysis Laboratory at Stephen F. Austin State University.

DATA ANALYSIS. Importance values were calculated using relative basal area (m^2) and relative density (number of trees/subplot) for overstory species (Muller-Dombois and Ellenberg 1974). Understory cover percentages from the ten 1 m^2 quadrats were averaged to obtain species cover per plot (Daubenmire 1968). Importance values of overstory species and understory cover percentages were arranged in Q matrices in which plots served as rows and species importance value/cover percentage served as columns. In addition, attribute (i.e., altitude, slope, aspect, slope position, pH, and soil nutrient content) data were arranged in a Q matrix. Attribute variables were adjusted to a normal (standard) deviate to remove the arbitrary effect of different attribute units (Romesburg 1984).

A total of 120 plots were classified using cluster analysis with two separate analyses for overstory and understory data. In cluster analysis, flexible beta linkage and Bray-Curtis coefficient (Sørenson distance) were used as a group linkage method and a distance measure, respectively. A value of $\beta = -0.25$ was chosen for the group linkage method. According to McCune and Grace (2002), a value of $\beta = -0.25$ produces results similar to those obtained using Ward's group linkage method. The resulting dendrograms were scaled using Wishart's objective function that measures loss of information at each step of cluster formation (McCune and Mefford 1999). Indicator Species Analysis (ISA) was utilized as an objective criterion for pruning overstory and understory dendrograms (Dufrêne and Legendre 1997, McCune and Grace 2002). Indicator values were obtained for each species at each step of cluster formation by multiplying relative frequency (proportion of sample units that contain the species in each group) by relative abundance (proportional abundance of the species in each group) and expressing the outcome as a percentage. Statistical significance of indicator values was assessed using a Monte-Carlo randomization test with 10,000 permutations. Optimum number of clusters was chosen based on maximum number of significant indicators and minimum average *P* value (McCune and Grace 2002). ISA was also utilized to identify characteristic or indicator species within each of the final overstory and understory groups. Only species with significant ($P \leq 0.05$ level) indicator values that were equal to or greater than 24% were regarded indicator species within each group.

Overstory and understory data were separately subjected to Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Principal Coordinate Analysis (PCoA). Bray-Curtis coefficient was used as the distance measure for PCoA. In CA and DCA, the option of downweighting rare species was selected. All analyses, except PCoA, were performed using PC-ORD software (McCune and Mefford 1999). PCoA was performed using the program PCO (Anderson 2003). To relate vegetation patterns (overstory and understory) to the measured attribute variables, joint plot overlays were constructed utilizing the attribute data matrix as a secondary matrix in PC-ORD (McCune and Mefford 1999). In joint plot construction, PC-ORD's default cut-off coefficient of determination (r^2) value of 0.20 was used. Attribute variables with r^2 values greater than 0.02 were shown as vectors within the ordination graph. Vectors indicate which, if any, of the attribute variables measured explain a portion of the variation represented by an axis. In addition, Pearson's (r) correlation coefficients were obtained for each attribute variable with each ordination axis scores. To evaluate the quality of DCA ordinations, an after-the-fact evaluation of the variance represented by each axis was performed by calculating coefficient of determination values between distances in the ordination space and distances in the original unreduced space (McCune and Mefford 1999). In after-the-fact evaluation, ordination space distances were measured as Euclidean distance whereas distances in the original unreduced space were measured as relative Euclidean (McCune and Grace 2002).

Results. For overstory data, maximum number of significant indicators (5 species) and minimum average *P* value (0.0097) were achieved by pruning the dendrogram at the 43.75% information remaining level, which resulted in four clusters (Fig. 1). Indicator values allowed for the identification of characteristic species within each overstory cluster (Table 1). Within each cluster, species with high indicator values reflected high faithful-

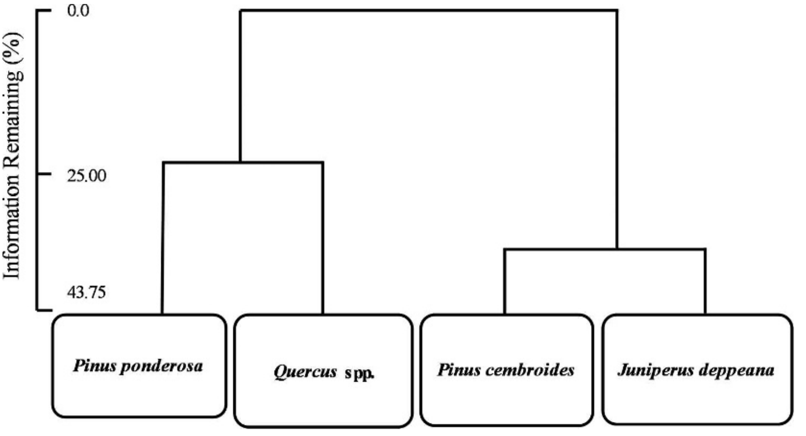

FIG. 1. Cluster analysis dendrogram of overstory data, using Sørenson distance and flexible beta (−0.25) linkage method, cut at 43.75% of the information remaining scale. Indicator species (INDVAL ≥ 24 and $P \leq 0.05$) were used to label the groups.

ness and exclusiveness to that cluster. *Pinus ponderosa* was identified as an indicator species for the first cluster whereas *Pinus cembroides*, *Quercus* spp., and *Juniperus deppeana* were identified as indicator species for the second, third, and fourth clusters, respectively. Importance values of those species corresponded with their identification as indicator species for each cluster (Fig. 2). For understory data, maximum number of

Table 1. Indicator species within each overstory and understory cluster with their corresponding maximum observed indicator values (% in bold) and *P* values.

Stratum	Species	Cluster 1	2	3	4	5	6	7	8	*P* value[b]
Overstory	*Arbutus xalapensis*	13	2	23	0	-	-	-	-	0.0476
	Juniperus deppeana	17	17	19	**46**	-	-	-	-	0.0001
	Pinus cembroides	17	**41**	12	29	-	-	-	-	0.0001
	Pinus ponderosa	**55**	13	21	7	-	-	-	-	0.0001
	Quercus spp.	20	25	**39**	16	-	-	-	-	0.0001
Understory	*Baccharis salicifolia*	0	0	0	0	0	**24**	0	0	0.0113
	Bouteloua curtipendula	1	0	0	7	4	9	24	**43**	0.0001
	Bouteloua hirsuta	0	0	0	2	0	3	9	**66**	0.0001
	Carex praegracilis	15	1	0	3	6	7	3	**32**	0.0015
	Chamaesyce nutans	0	0	0	4	1	3	2	**44**	0.0003
	Cologania angustifolia	5	6	5	6	9	11	**30**	27	0.0016
	Cologania pallida	3	1	0	**24**	19	0	1	6	0.0349
	Cuperus manimae	13	0	0	6	2	3	7	**26**	0.0065
	Dichondra aregentea	0	0	1	1	0	0	**24**	6	0.0435
	Erigeron spp.	1	0	0	1	0	0	0	**39**	0.0005
	Evolvulus sericeus	0	1	0	0	0	1	6	**43**	0.0001
	Hieracium fendleri	14	**27**	4	10	7	2	2	0	0.0055
	Ibervillea lindheimeri	2	0	0	2	**24**	2	0	0	0.0142
	Muhlenbergia emersleyi	6	13	**35**	10	21	7	4	2	0.0001
	Muhlenbergia pauciflora	**30**	22	6	2	8	5	12	0	0.0018
	Muhlenbergia rigens	0	0	0	1	0	**74**	0	11	0.0001
	Oenothera brachycarpa	0	0	0	0	0	3	0	**24**	0.0073
	Panicum spp.	0	0	0	2	0	0	1	**34**	0.0018
	Pinus ponderosa[a]	8	12	**24**	3	3	1	1	0	0.0309
	Piptochaetium fimbriatum	16	8	10	7	11	9	**29**	10	0.0001
	Quercus spp.[a]	9	**32**	14	12	6	6	5	5	0.0005

[a] Overstory seedlings.

[b] Proportion of permutations with a maximum indicator value that is equal to or greater than the maximum observed indicator value.

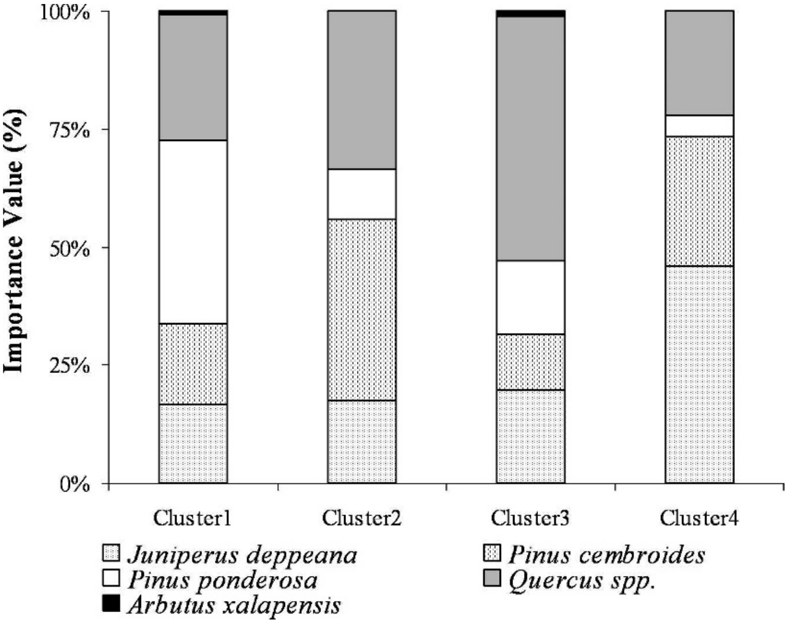

FIG. 2. Mean percentage importance values of overstory species in each cluster as identified by cluster analysis at the chosen cut level of 43.75% of the information remaining scale.

significant indicators (38 species) was achieved at four clusters whereas minimum average *P* value (0.2404) was achieved at nine clusters. As a compromise (36 significant indicators and average *P* value of 0.2406), the understory dendrogram was pruned at the 25.0% level of the information remaining scale, which resulted in eight clusters (Fig. 3). One or more indicator species characterized each understory cluster (Table 1). Overstory and understory groups were combined into 13 associations that were named using indicator species of each group (e.g., *Pinus ponderosa-Muhlenbergia pauciflora* Buckl.) (Fig. 4).

For the overstory, the first two CA ordination axes represented 74% of the total variation whereas DCA and PCoA first two axes represented 77% and 82% of the total variation, respectively (Table 2). In each of the ordination graphs, overstory groups were clearly separated in the space identified by the first two axes (Fig. 5). The first axis differentiated between *Pinus ponderosa* and *Juniperus deppeana* communities. The second axis contrasted between *Juniperus deppeana* and *Pinus ponderosa* communities on the one hand and *Pinus cembroides* and *Quercus* spp. communities on the other. For CA and DCA, none of the measured attribute variables were strongly correlated ($|r| < 0.4$) to the first axis. However, three variables namely altitude, slope position, and slope inclination were strongly ($|r| \geq 0.4$) negatively correlated to the second axis. For PCoA, none of the measured variables had an absolute correlation coefficient with the any of the first two axes that was greater than 0.2 except for altitude, which had an *r*-value of 0.3 with the first axis.

For the understory, the first two ordination axes represented 20%, 44%, and 33% of the total variation for CA, DCA, and PCoA, respectively (Table 2). In each of the ordination graphs, the first axis differentiated between *Bouteloua hirsuta* Lag./*Evolvulus sericeus* Sw., *Muhlenbergia rigens* (Benth.) A.S. Hitchc./*Baccharis salicifolia* (Ruiz and Pavón) Pers., and *Cologania angustifolia* Kunth/*Piptochaetium fimbriatum* (Kunth) A.S. Hitchc. communities on the one hand and *Muhlenbergia emersleyi* Vasey/*Pinus ponderosa* and *Quercus* spp./*Hieracium fendleri* Schultz-Bip. on the other (Fig. 6). *Muhlenbergia pauciflora*, *Cologania pallida* Rose, and *Ibervillea lindheimeri* (Gray) Greene occupied an intermediate position along the first axis. In all ordination methods, the second axis represented a minor portion of the total variation and thus was

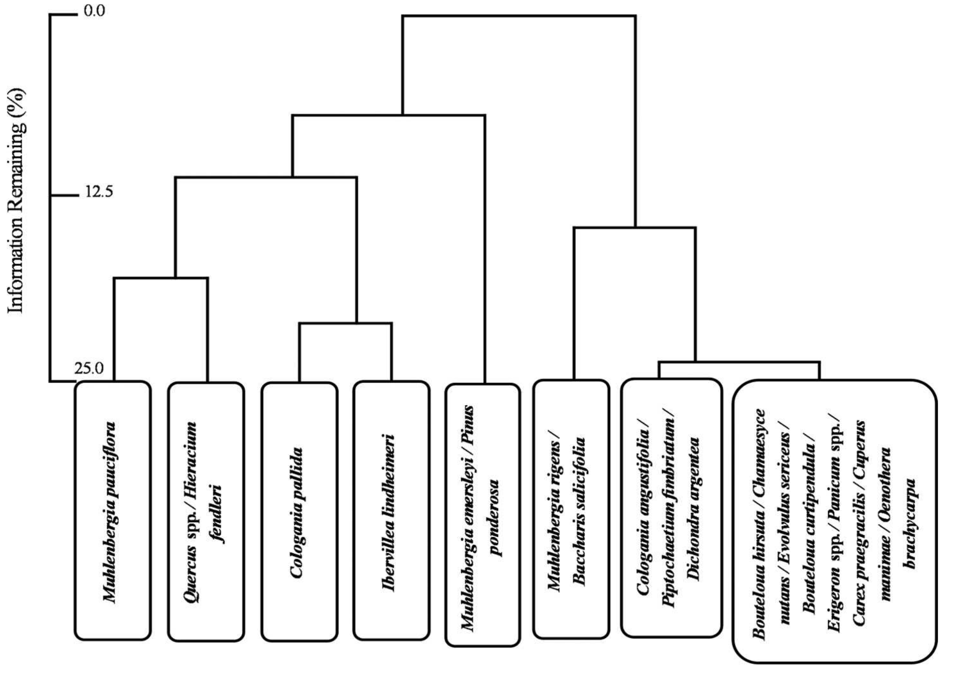

FIG. 3. Cluster analysis dendrogram of understory data, using Sørenson distance and flexible beta (−0.25) linkage method, cut at 25.0% of the information remaining scale. Indicator species (INDVAL ≥ 24 and $P \leq 0.05$) were used to label the groups.

considered unimportant in the interpretation. Moreover, understory groups did not reflect clear separation along the second axis. For CA and DCA, the three aforementioned attribute variables were strongly negatively correlated to the first axis and none of the measured attribute variables were strongly correlated to the second axis. For PCoA, altitude ($r = 0.6$)

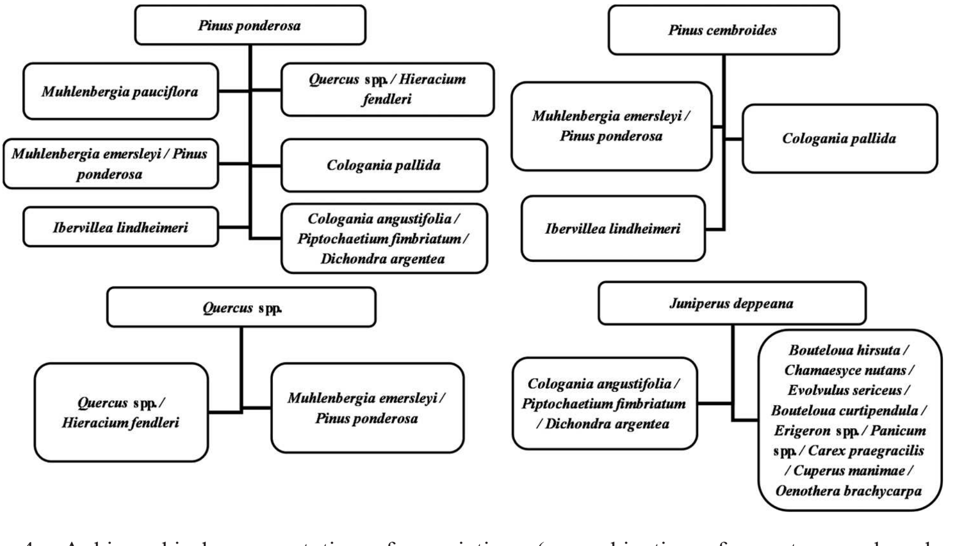

FIG. 4. A hierarchical representation of associations (a combination of overstory and understory groups).

Table 2. Proportion of variance represented by each of the first two axes of Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Principal Coordinate Analysis (PCoA).

Stratum	Axis	CA	DCA[a]	PCoA
Overstory	1	0.53	0.62	0.56
	2	0.21	0.15	0.26
	Cumulative	0.74	0.77	0.82
Understory	1	0.13	0.31	0.21
	2	0.07	0.13	0.12
	Cumulative	0.20	0.44	0.33

[a] Calculated as coefficient of determination (r^2) values between distances in the ordination space and distances in the original unreduced space.

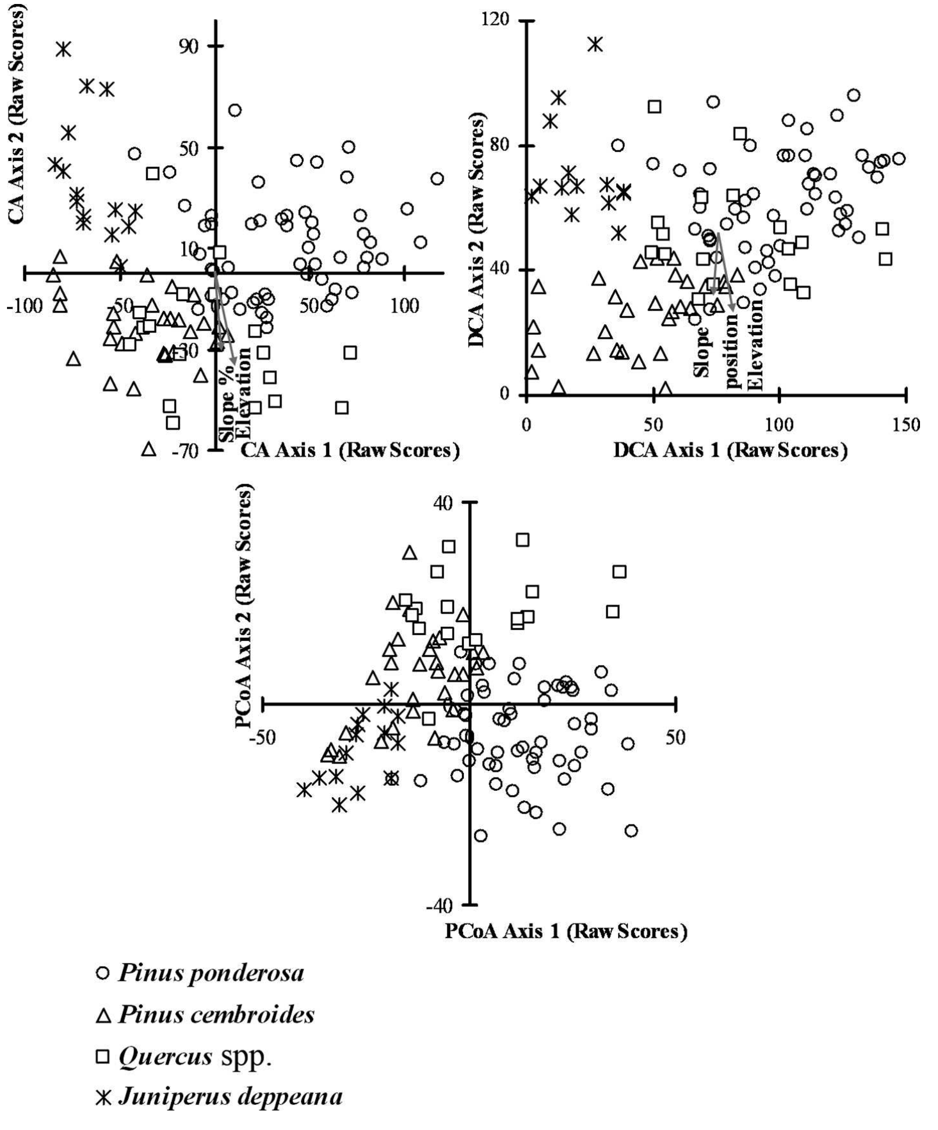

FIG. 5. Ordination graphs of the first two axes of overstory Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Principal Coordinate Analysis (PCoA). The symbols indicate overstory groups as identified by cluster analysis and the vectors represent attribute variables with r^2 values greater than 0.02 for CA and DCA graphs.

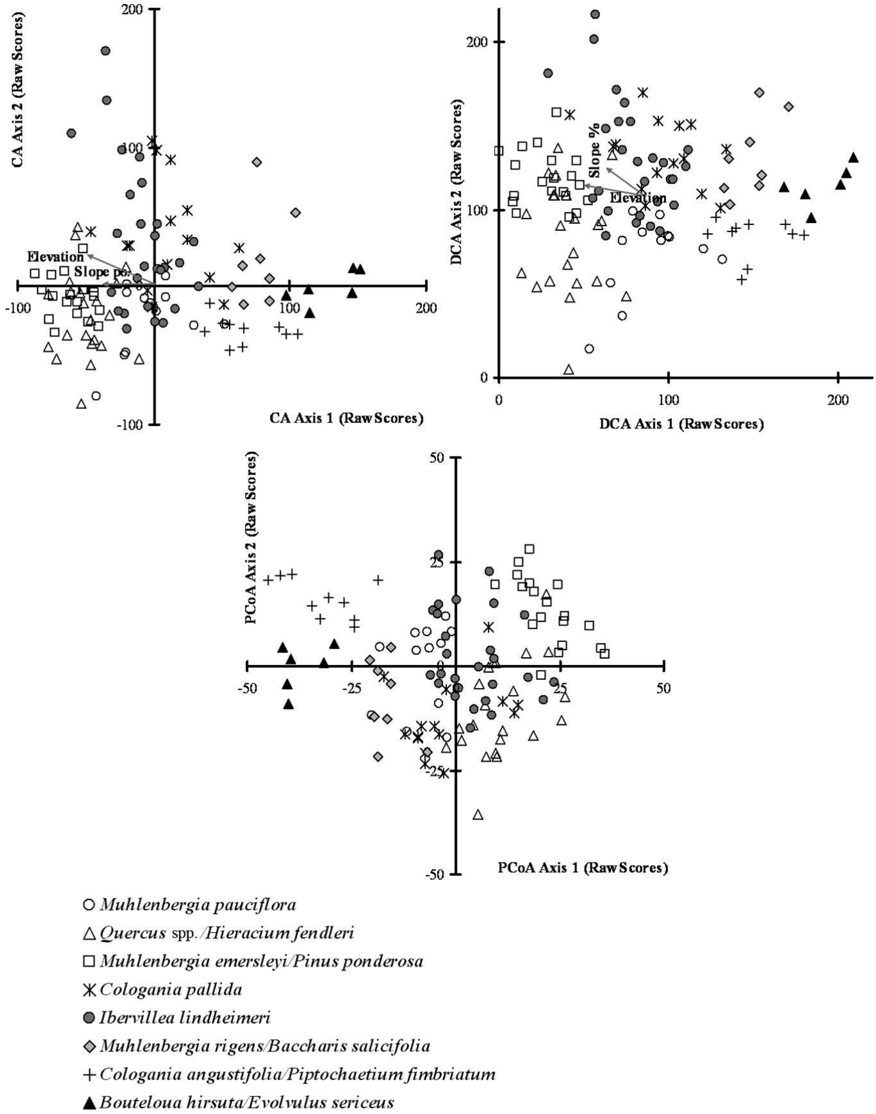

FIG. 6. Ordination graphs of the first two axes of understory Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Principal Coordinate Analysis (PCoA). The symbols indicate understory groups as identified by cluster analysis and the vectors represent attribute variables with r^2 values greater than 0.02 for CA and DCA graphs.

as well as Na content of the A-horizon ($r = -0.4$) were strongly correlated to the first axis. None of the measured attribute variables were strongly correlated to the second PCoA axis.

Discussion. Species composition of *Pinus ponderosa* forests of the Davis Mountains are similar to those found in other sky island forests of the southwestern United States. The plant communities associated with *Pinus ponderosa* in the Davis Mountains are similar to the plant communities found in Whittaker and Niering's (1965) 1830–2130 m elevation range of the Santa Catalina Mountains, except that the Davis Mountains plant communities include *Pinus ponderosa*. In comparison with Whittaker and Niering, *Pinus ponderosa* of the Davis Mountains occur at lower elevations (mean elevation range of 1819–1970 m versus 2130–2740 m). The *Pinus ponderosa* elevation range of the Davis Mountains is also lower than that reported by Gottfried et al. (1995).

Despite their apparent homogeneity, *Pinus ponderosa* forests of the Davis Mountains exhibit tremendous variation in local plant communities that could partially be explained by slight variation in some of the measured attribute variables (Figs. 5 and 6). Among the attribute variables evaluated in this study, altitude, slope position, and slope inclination were identified as primary components of a complex environmental gradient represented by the first and second axes of understory and overstory ordination graphs, respectively. The low correlation coefficient values of the measured attribute variables to the overstory ordination's first axis suggest that non-evaluated variables may be responsible for most of the discrimination among overstory groups (Fig. 5). Field observations from this study along with the distributional range of *Pinus ponderosa* suggest that *Pinus ponderosa* water requirements are greater than those of *Pinus cembroides* and *Juniperus deppeana*. According to Oliver and Ryker (1990), the most limiting factor to *Pinus ponderosa* growth, throughout its range, is soil moisture. Thus, *Pinus ponderosa* distribution on drier sites, such as the Davis Mountains, is strongly related to supplies of available soil moisture, which are related to soil texture and depth (Hodgson 1978). According to Gottfried et al. (1995), junipers are more drought-tolerant than pinyons and tend to dominate drier sites. Moreover, Allen and Breshears (1998) reported the encroachment of pinyon-juniper woodlands into *Pinus ponderosa* territories in New Mexico in response to severe droughts. Thus, the first axis may be interpreted as a moisture gradient in which *Pinus ponderosa* occupied wetter sites as compared to sites occupied by *Juniperus deppeana*. The second axis reflected physiographic variations along which *Juniperus deppeana* and *Pinus ponderosa* communities occupied low altitude gentle slope sites whereas *Pinus cembroides* and *Quercus* spp. communities occupied high altitude steep slope sites. When arranging overstory groups along an altitude gradient, the groups, ordered from highest to lowest, are *Pinus cembroides*, *Quercus* spp., *Pinus ponderosa*, *Juniper deppeana*. This is in contrast to Whittaker and Niering (1965) who found that *Pinus ponderosa* communities occur above *Pinus cembroides* and *Juniperus deppeana* communities of the Santa Catalina Mountains.

For understory, the first ordination axis reflected physiographic variation along which *Bouteloua hirsuta*/*Evolvulus sericeus*, *Cologania angustifolia*/*Piptochaetium fimbriatum*, and *Muhlenbergia rigens*/*Baccharis salicifolia* communities occupied low altitude gentle slope sites whereas *Muhlenbergia emersleyi*/*Pinus ponderosa* and *Quercus* spp./*Hieracium fendleri* communities occupied high altitude steep slope sites (Fig.6). Although slight variation in physiographic attributes may help explain the observed vegetation pattern, it is important to emphasize that those physiographic attributes may not be but a surrogate to other more important attribute variables such as soil depth. For example, the presence of deeper colluvium soils towards the bottom of slopes may result in the retention of higher amounts of soil moisture and soil nutrients which would play a more important role in influencing species distributions than that of mere altitude or slope inclination. In fact, examination of species amplitudes indicates that species such as *Dichondra argentea* Humb. & Bonpl. ex Wild. and *Panicum bulbosm* Kunth that are common to open sunny sites with well drained soils were characteristic of *Juniperus deppeana* associations (Powell 1998) (Figs. 4 and 6). This may suggest that the first axis is merely a reflection of a soil moisture gradient in which *Juniperus deppeana* associations occupied the drier sites whereas *Pinus ponderosa* associations occupied the wetter sites. According to Bassman (1987), *Pinus ponderosa* is considered a drought tolerant species, but high salt concentrations affect the growth of the root system. High Na content of the A-horizon for *Juniperus deppeana* associations may support this interpretation.

Conclusions. *Pinus ponderosa* forests of the Davis Mountains were classified into four overstory groups and eight understory groups the combination of which resulted in 13 associations. Since vegetation is the product of many environmental factors, several environmental variables were examined to help explain possible differences among the associations. The major environmental factors contributing to the variation in local vegetation patterns of the Davis Mountains are altitude, slope position, slope inclination, and soil moisture. These environmental factors were used to help describe the differences among the associations classified in this study.

It should be noted, however, that attempts to extract major environmental gradients are just a simplification of the true picture. In fact, the extracted gradients (e.g., altitude) are themselves complex gradients of many interrelated variables such as sun exposure, temperature, soil depth, humidity, drainage pattern, and so forth. It is suggested, however, that a direct gradient analysis, in which moisture, altitude, soil depth, soil texture, and a few more potentially important environmental variables are measured, be conducted within the Davis Mountains.

This study was an initial survey of the plant communities associated with *Pinus ponderosa* in the Davis Mountains. The results of this study may be used in the future to place experimental units in similar areas based on overstory, understory, and environmental variables. This placement will facilitate the collection and interpretation of research results. In addition, results from future studies regarding management practices in these plant communities can be extrapolated and used by land managers in the Davis Mountains with similar plant communities.

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