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Understory Species as Soil Moisture Indicators in Oregon's Western Cascades Old-Growth Forests

Abstract

Soil moisture regimes are influenced by a complex array of biotic, edaphic, and topographic factors. Understory species provide the potential to depict landscape-scale moisture patterns because they integrate across these influences in both time and space. We examined the relationship between soil moisture and understory species in old-growth Douglas-fir, true fir, and Douglas-fir/true fir transition forests in the H. J. Andrews Experimental Forest, located in the Western Cascades of Oregon. Using multivariate statistical analyses, we determined that a quick survey of understory vegetation could provide reasonable estimates of relative spatial differences in soil moisture. Classification analysis separated the understory species into two communities that were differentiated primarily along an elevation (temperature) gradient, and the high elevation community had wetter soil on average. Within these communities, individual species could be used as indicators of relative moisture differences. Our data support the existing habitat typing model for this region that elevation (temperature) and moisture are the main determinants of vegetation zones and associations. They also suggest that understory species are sensitive enough to be used as soil moisture indicators even in a predominantly mesic watershed.

Introduction

Plant distributions in the Western Cascades are thought to be primarily influenced by gradients of temperature. Much has been researched on the relationship between temperature and diversity, occurrence, and abundance of plants in these forests (Brockway et al. 1983, Topik et al. 1986). Dyrness et al. (1974) proposed that forests in the central Western Cascades have three vegetation zones, distributed along an elevation gradient. Plants do not respond directly to elevation, per se, but rather to temperature, which is related to elevation and has a direct effect on physiological processes.

Soil moisture also varies along elevation gradients and can influence many ecological processes in these forests (Bailey et al. 1998, Brockway 1998, Franklin and Halpern 2000). Photosynthesis, respiration, and nutrient uptake, depend upon soil moisture, and it acts as a primary constraint to forest site productivity (Band et al. 1993, Vertessy et al. 1996). Moisture levels also play a major role in determining forest flammability and thus are critical to determining fire regime and fire hazard ratings (Clark 1990, Minnich and Chou 1997). Variability in soil moisture should be considered in forest management decisions. For example, when decisions are required regarding the allocation of limited resources (e.g., selecting sites for fire hazard abatement measures, choosing between potential harvest units), a high quality index of relative soil moisture would be an extremely useful management tool.

Many factors in addition to elevation influence soil moisture, and developing a good, predictive soil moisture index and map could take several years. Mapping soil moisture is complicated because point-specific wetness depends on a multitude of factors, some of which are difficult to measure. For example, soil moisture varies with elevation, but there are many characteristics, such as topography, soil structure and capillary action, which create relative differences in soil moisture within a given elevation zone (Ambroise 1995). Methods for estimating soil moisture using proxy indices that do not rely on direct moisture measurements have become increasingly common (Grayson and Western 2001). Field-based indices include such variables as yearly rainfall, soil type, hillslope, and aspect. Additional indices can be derived from digital elevation models (DEMs),

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such as topographic convergence, which estimates soil moisture based on potential drainage into and out of an area (Beven and Kirkby 1979). Knowledge of the topographic and edaphic properties of an area can be combined to create soil moisture maps at the landscape level (Iverson et al. 1997, Naden et al. 2000), but many problems confound these landscape-scale models. While topography can be modeled relatively easily, factors such as soil composition and depth must actually be measured. It can take years of work to develop a model that includes all of the factors that potentially influence soil moisture, and even more time to determine how to weight the different factors appropriately, given that each may be more or less influential in different areas.

An alternative to estimating spatial soil moisture patterns indirectly from topographic and edaphic variables is to measure soil water directly in the field. Synoptic handheld time domain reflectometry (TDR) probes are popular for field sampling, but are expensive and time consuming and do not capture changes over time or space without multiple sampling (Noborio 2001). TDR probe measurements are affected by fine-scale changes in light level, soil composition, and topography, which can present problems in integrating a few point samples to the stand level and beyond. A method is needed that not only accounts for multiple influences on the water balance, but also integrates across space and time. To cover large landscapes, this method should be simple to implement and relatively inexpensive.

The analysis of understory species is a possible quick method to measure relative wetness at the stand and landscape scales. Plants integrate over space and time, and could provide a smooth, sensitive map of an area's moisture regime. They are everywhere on the forest floor and, theoretically, each stem acts as a natural TDR probe. Herbaceous species that only grow within a narrow range of soil moisture levels are the best indicators (Rowe 1956). A quick survey of the dominant vegetation growing on the forest floor may be a better gauge of soil moisture patterns than scattered TDR values or more abstract DEM-based models. Previous studies have successfully employed this indicator species approach to a variety of ecosystems (Wang 2000, Salmela et al. 2001). We investigate whether this approach can be used in old-growth forests of Oregon's Western Cascades. A defining feature of the Western Cascades is that nearly all the forests in this area are considered mesic. Therefore, we attempt to determine whether indicator plants may provide an index sensitive enough to differentiate these relatively subtle differences in moisture.

Methods

Study Site

The H. J. Andrews Experimental Forest (HJA) is located on the west slope of the Cascade Mountains (Figure 1). It comprises the Lookout Creek watershed, 80 km east of Eugene, Oregon. The Long Term Ecological Research (LTER) site covers 6400 ha and ranges in elevation from 410 m to 1630 m (McKee 1998). The watershed lies within the Blue River Adaptive Management Area, one of 10 such areas devoted to the development and evaluation of progressive management strategies for northwestern forests (Cissel et al. 1999). At the time of its establishment in 1948, the HJA was an intact forest with about 65% of the land in old-growth forest (i.e., 400-500 yr old). Since that time, old-growth forest has been reduced to 40% of the total area due to logging activities.

Climate at HJA is characteristic of the Pacific Northwest, with dry summers and wet winters. Annual precipitation ranges from 2200 mm at the base station to 3400 mm at upper elevations, with less than 300 mm normally falling during the summer growing season (Grier and Logan 1977). Soils are mostly deep, well-drained Inceptisols. Rooting occurs almost entirely in the upper 200 cm of soil. Textures range from gravelly, silty clay loam to very gravelly, clay loam (Grier and Logan 1977). Lower elevation soils are older than upper elevation soils, dating back to the Oligocene-lower Miocene. Upper elevation soils are composed of younger andesite lava flows and High Cascade rocks.

Zobel et al. (1976) argued that topography is more important than soil differences in controlling vegetation in this region. Douglas-fir *(Pseudotsuga menziesii)*, western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) are the dominant species at lower elevations, while Pacific silver fir (*Abies amabilis*), noble fir (*A. procera*), and mountain hemlock (*T. mertensiana*) dominate upper elevations (Franklin and Dyrness 1988). On a regional basis, elevation and associated

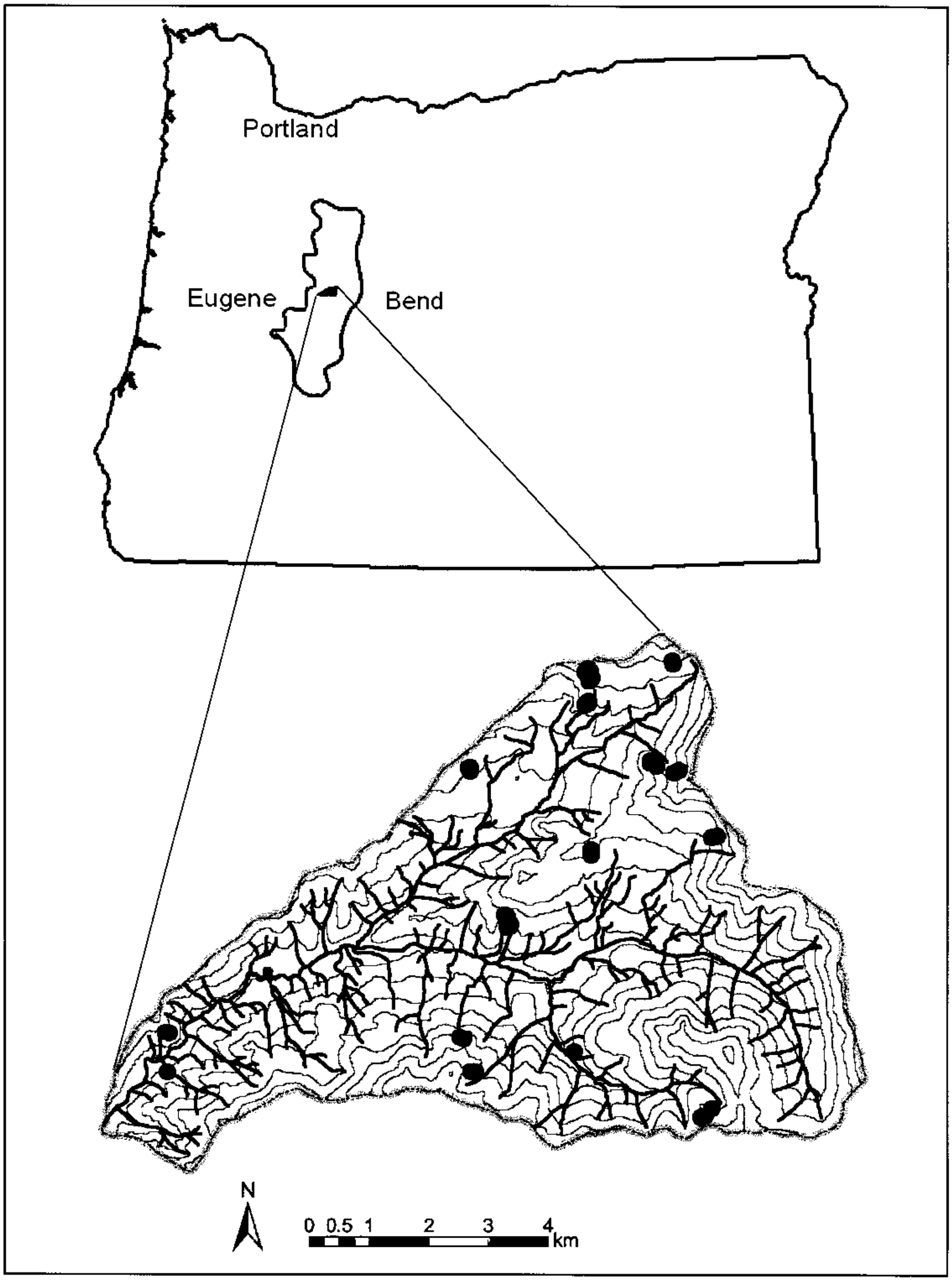

Figure 1. The H. J. Andrews Experimental Forest Long Term Ecological Research site, located on the west side of the Cascade Mountains, 80 km east of Eugene, Oregon. Black circles represent the 60 study plots overlaid on a 100-m contour map.

macroclimate also are the major correlates with community composition throughout Oregon (Ohmann and Spies 1998).

Data Collection

We collected georeferenced data on vegetation and site characteristics at 60 plots distributed throughout the HJA (Figure 1). The 20x20 m plots were located in Douglas-fir/western hemlock stands, Pacific silver fir/noble fir stands, and transition areas between these two forest types. We attempted to collect an equal number of samples from each forest type, which skewed our collection towards the upper elevations in our study area (Figure 2).

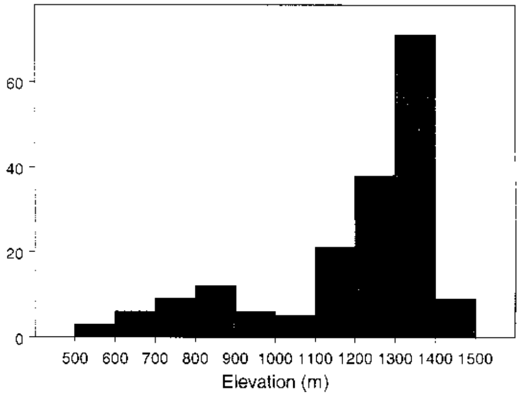

Figure 2. Elevation data for 180 2 x 2 m sample quadrats. Counts are distributed evenly among the dominant forest types in the study area.

Topographic variables collected on the plots included slope, aspect, and slope angle in each of the four cardinal directions. Aspect was transformed to a more direct measure of heat load on a scale of –1.0 (northeast-facing slopes) to +1.0 (southwest-facing slopes) (Taspect = -cos(45-Aspect)) (Beers et al. 1966). Slope measurements in the cardinal directions were averaged to generate a Terrain Shape Index (TSI) (McNab 1989), which ranged from –12.75 to +14 with positive numbers indicating coves and negative numbers indicating domes. Elevation was derived from GPS measurements and ranged from 493 m to 1439 m. A Topographic Convergence Index (TCI) (Beven and Kirkby 1979) was calculated from a DEM based on the local slope angle and upslope contributing area of the plot.

Information on the soil content and structure also was collected at 35 sites. At each site, soil depth, to a maximum of -100 cm, was recorded at 1 m intervals along three 10 m transects. One soil sample was collected at a random location along each of the three transects. These samples were air-dried and sealed for laboratory analysis of soil texture. In the laboratory, soil samples were passed through a 2 mm screen to remove large rocks and other debris. Soil texture analysis was conducted using a sedimentation method on the 2 mm fraction (Sheldrick and Wang 1993).

A random number generator was used to place three vegetation sampling quadrats in each plot. For each 2x2 m quadrat, we determined the three most dominant understory species. In most cases, these species composed over 90% of the total understory vegetation coverage as recommended by Norman and Streiner (2000) for the truncation of data to remove rare species. Each species was assigned a relative percent ground cover value, and quadrats were relativized by total cover for the three species so that the sum of the relative cover values in each quadrat equaled 1.0. The dominant species and percent cover values were cross-referenced among at least two people to ensure consistency.

Volumetric soil moisture was measured with handheld Hydrosense TDR probes from 10-23 July 2002. We chose the dry season for our moisture sampling for logistical reasons and because we were interested in soil moisture patterns at the peak of the growing season. Three readings were taken in each quadrat, and then averaged. To determine canopy coverage, spherical densiometer readings were taken in the four cardinal directions, standing in the middle of each quadrat.

Data Analysis

Correlation analysis was conducted to compare the ability of different environmental proxy indices to predict soil moisture content. We aggregated moisture measurements from the three quadrats per plot for this analysis, because most of our environmental data were available at only the plot level. We examined the correlation between soil moisture and the following common indicators of soil moisture: elevation, TCI, TSI, Taspect, slope, soil properties, and canopy cover.

We next examined the ability of understory communities and individual species to predict soil moisture levels. Vegetation survey data from the individual quadrats were compiled into a master list of all species observed in the study area. Species that occurred in less than 10 quadrats were discarded. For each remaining species, we averaged the TDR measurements for all quadrats on which the species was found to attain mean soil moisture values for the species.

A hierarchical clustering analysis was conducted on the vegetation data to partition the data into discrete groups or communities. Clustering analyses identify natural breaks or groups in a data set (Sneath and Sokal 1973). The approach sequentially merges plots (agglomerate) with similar species characteristics. These analyses are highly dependent upon the choice of distance measure used to assess group similarity and the linkage criteria used to determine the distance between groups for joining purposes (Legendre and Legendre 1998). In this analysis, we relied upon the Bray-Curtis index (Bray and Curtis 1957) as a measure of dissimilarity for all analyses of species abundance patterns (see Legendre and Legendre 1998 for a comprehensive discussion of potential dissimilarity indices). Measured as percent dissimilarity, the index provides ecological distance between samples as elements of a secondary data matrix. Unweighted pair-group method arithmetic (UPGMA) was used as the joining criteria for the analysis (Sneath and Sokal 1973). UPGMA averages all distances equally for all possible groups. This linkage method minimized the chaining of the resultant dendrogram (2.9%).

We conducted an indicator species analysis (Dufrene and Legendre 1997) on the quadrats to identify key species for the clusters. Indicator species analysis identifies species with high fidelity for a single group (i.e., an indicator of the group). Indicator values combine information on species relative abundance and relative frequency in different groups. Relative abundance is calculated as the mean abundance of a species in a given group of quadrats divided by the mean abundance of that species in all quadrats. Relative frequency is calculated as the percentage of quadrats in a given group where a species is present. Indicator values range from 0 to a maximum of 100 for a perfect indicator. Species were assigned to the cluster for which they had the highest indicator score.

For visual interpretation of the classification analysis, clusters were mapped into ordination space using canonical correspondence analysis (CCA) (ter Braak 1986, Palmer 1993). The objective of any ordination is to orient the objects in such a way that proximity in ordination space resembles proximity in ecological space. CCA constrains the ordination of species by a multiple linear regression on a second environmental matrix; thus, it is not free to express all of the structure in the community data. It can be appropriate if the objective is to describe community variation with respect to a particular set of measured environmental variables (McCune and Grace 2002). In this case, we were interested in testing the relationship between the understory indicators and soil moisture. We included elevation in the analysis as well, as a proxy for temperature variability. Thus we expected to derive empirically an ordination diagram that resembles an ordering of plant communities along temperature and moisture axes (Dyrness et al. 1974).

We tested for significant correlations between the species data matrix and the elevation/soil moisture data matrix along each of the axes using a Monte Carlo simulation with 1000 randomization runs. For each run, the rows were randomly reassigned within the environmental data matrix destroying the relationship between the two matrices. The correlation coefficients from the actual data then were compared to those derived from the randomized matrices.

The program PC-ORD version 4.09 (McCune and Mefford 1999) was used to conduct all clustering and ordination analyses. S-PLUS 2000 (Mathsoft, Incorporated) was used for all other statistical analyses. The significance level was set at $P = 0.05$.

Results

Soil moisture content varied from 5-34% over the study area with a mean value of 13.4% and a standard error of 0.3 ($N = 540$). No substantial rain events were observed during the study period and permanent datalogger stations within the HJA showed a mean decrease of 2.3% over the nearly 2-wk period.

Elevation was the only potential environmental proxy variable significantly correlated with measured soil moisture ($P = 0.022$; Table 1). Higher elevations, on average, had higher soil moisture.

TABLE 1. Pearson product moment correlation coefficients (r) of potential environmental influences on soil moisture with measured soil moisture values. Elevation is the only variable significantly correlated with soil moisture. $N = 60$ plots.

Environmental Variables	Correlations with Soil H_2O (r)
Elevation	0.29
Slope	-0.13
Transformed Aspect	-0.06
Topographic Convergence Index (TCI)	0.18
Terrain Shape Index (TSI)[1]	0.04
Canopy Cover	0.05
Soil Depth	0.02
Litter Depth[1]	0.09
Percent Silt[1]	0.22
Percent Sand[1]	-0.16

[1]data available for only 35 plots.

TABLE 2. Indicator values for major vegetation groups. Indicator values are the percent of perfect indication, based on combining the values for relative abundance and relative frequency. * indicates significance at $P < 0.05$ level; ** indicates significance at $P < 0.005$ as determined by Monte Carlo analysis.

	Indicator Value	Relative Abundance	Relative Frequency
Group 1 (73 quadrats)			
Dwarf Oregon grape	53**	97	55
Prince's pine	35**	98	36
Salal	26*	100	26
Twinflower	25*	100	25
Sword fern	23*	99	23
Pacific blackberry	7	56	12
Group 2 (73 quadrats)			
Vanilla-leaf	40**	85	47
Bunchberry	33*	95	34
False Solomon's seal	27*	99	27
Foamflower	24*	88	27
Wild ginger	21*	87	25
Beargrass	13*	91	14
Oregon bedstraw	10	72	14
Snowberry	10	88	11
Inside-out-flower	9	85	11
Vine maple	9	70	12
Pathfinder	6	57	11
Group 3 (12 quadrats)			
White-veined wintergreen	99**	99	100

Though the signs of the correlation coefficients between soil moisture and the other environmental variables examined were in the directions predicted, none of these relationships was significant (Table 1).

Forty-nine understory species were observed on the plots. Eighteen met the criteria of being present in at least 10 of the 180 quadrats. Twelve of these were significant indicator species (Table 2). Seventy-three quadrats were assigned to both Group 1 and Group 2 by the classification analysis. The mean elevation of Group 1 quadrats (1016 m) was significantly lower than the mean elevation of Group 2 quadrats (1309 m). Group 1 was also significantly drier than Group 2 (mean soil moisture contents of 12.9% and 14.3%). Twelve quadrats clustered in close spatial proximity between 1315 m and 1333 m in elevation were assigned to Group 3, and the remaining 22 quadrats had none of the 18 species included in the analysis.

Axis 1 of the CCA ordination strongly partitioned the communities (Figure 3a). The structuring of this axis was influenced primarily by elevation (intraset correlation coefficient (ter Braak 1986) between elevation and Axis 1 = 0.99). Soil moisture had a weaker influence on this axis (r = 0.32), and plots were arranged predominantly along an elevation gradient.

Axis 2 was influenced primarily by the soil moisture variable (correlation between soil moisture and Axis 2 = 0.95; between elevation and Axis 2 = -0.04). The two main plant communities were not differentiated along this axis, but rather individual species within the communities were differentiated within the ordination space (Figure 3b).

The significance of the relationship between the species data and the environmental data along the different axes was tested through Monte Carlo simulation. The distribution of understory species was correlated strongly with the environmental data along both Axis 1 ($r = 0.88$; $P < 0.001$) and Axis 2 ($r = 0.43$; $P < 0.001$).

An ordination analysis on only the Group 2 data revealed that the influences of elevation and soil moisture were more orthogonal for these higher elevation samples than for the Group 1 samples (Figure 4). The ordering of species along Axis 2 in Figure 4b closely resembled the gradient in mean soil moisture from Oregon bedstraw (*Galium*

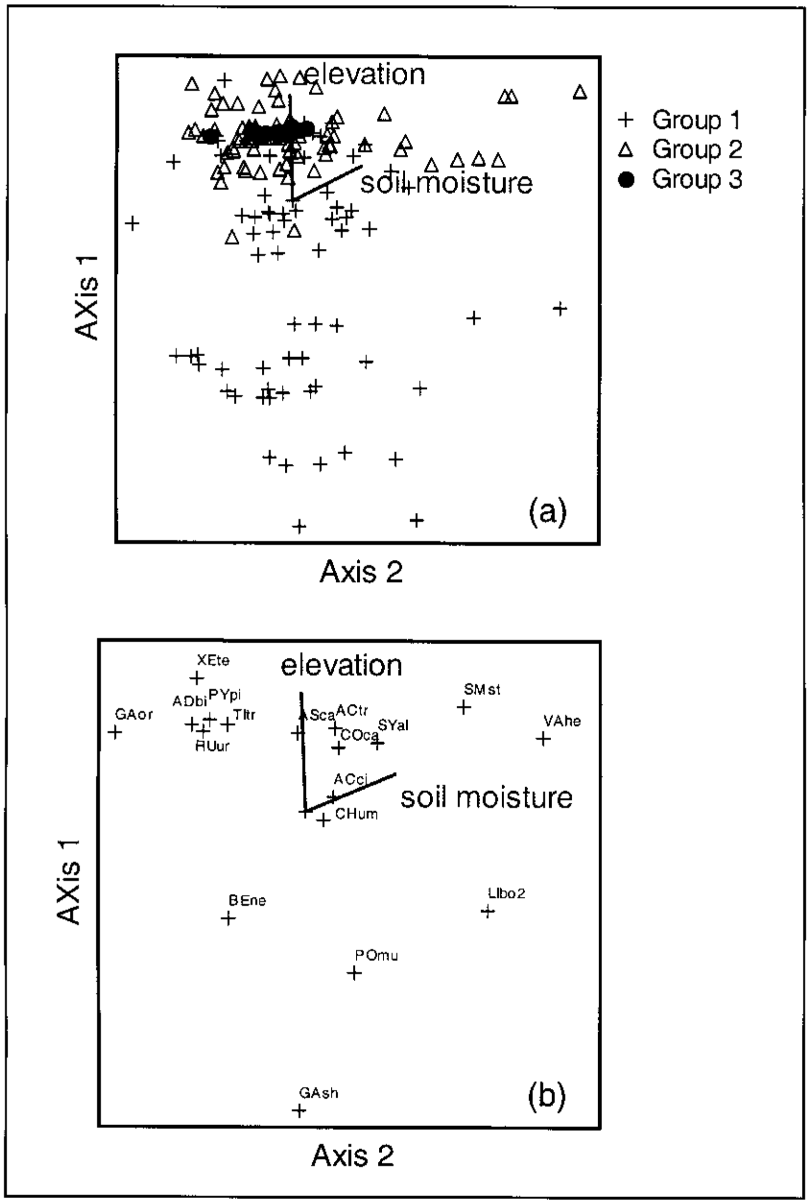

Figure 3. Canonical Correspondence Analysis constrained by elevation (an estimator of temperature) and mean measured soil moisture. Group labels correspond to the groups described in Table 2. Figure 3b provides the mean location of species observations in this ordination space. Species labels are first two letters of genus name followed by first two letters of species name.

oreganum) and pathfinder (*Adenocaulon bicolor*) to inside-out-flower (*Vancouveria hexandra*) reported for the upper elevation species in Table 3. The ordering of lower elevation species along Axis 2 (Figure 4a) did not correspond as directly to the overall moisture gradient observed for these species, because soil moisture also varied with the elevation gradient (Axis 1) in these plots. The differences in mean soil moisture for the individual species were significant (Table 3; $P < 0.001$).

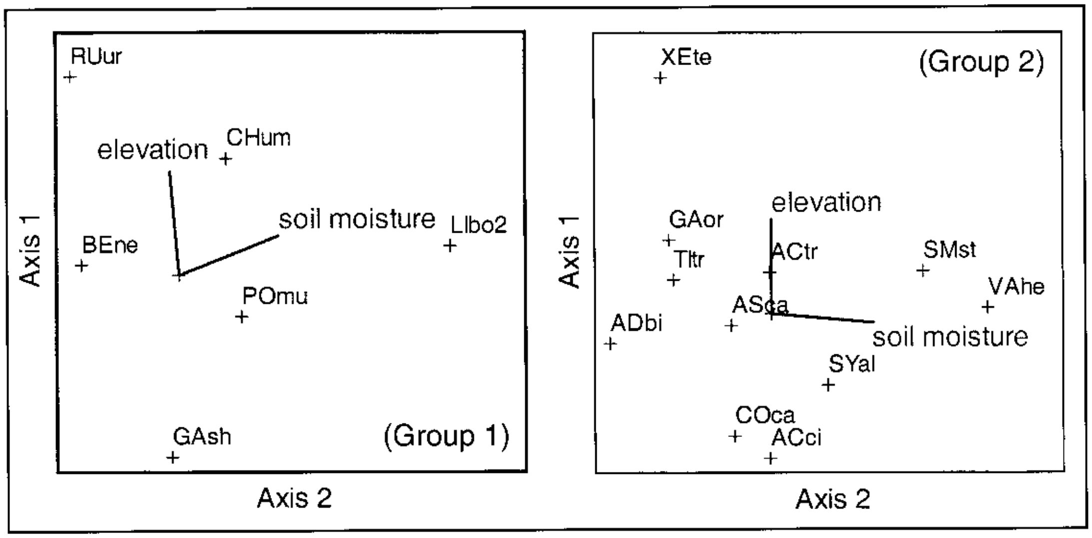

Figure 4. Canonical Correspondence Analyses for Group 1 and Group 2 separately. Only the quadrats identified by the classification analysis and the species identified by the indicator species analysis are included in the CCA of a given group.

Discussion

Our analysis contributes to the growing body of research in the use of understory species as soil moisture indicators. The multivariate results suggest that the two major understory communities in our study area are separated primarily along an elevation (temperature) gradient (Figure 3a), but because elevation is correlated with soil moisture (Table 1), the distribution of communities (Figure 3a) and species (Figure 3b) along the elevation gradient is also informative of spatial patterns in soil moisture. Soil moisture was not important to Axis 1 for the upper elevation group (Figure 4b), however, and others have shown that forest plant diversity in the Western Cascades is primarily influenced by gradients of temperature and secondarily by moisture (Brockway 1998).

Axis 2 of the ordinations focused on the variability in moisture after controlling for elevation (temperature). In other words, the indicator species listed in Table 2 provide a small subset of the dozens of understory species found in the Western Cascades that could be used to identify major vegetation zones as proposed by Dyrness et al. (1974). Our study shows that in addition to being warmer, the lower elevation zone is generally drier than the upper elevation zone during the summer. Further assessment of relative moisture levels could be made by comparing the individual species found at different locations within a vegetation zone. For example, species from the upper elevation vegetation zone are arrayed along a soil moisture gradient on Axis 2 of Figure 4b. The mean soil moisture for the species within this group ranges from 12.4% to 16.8%. Table 3 provides a summary of the general moisture affinities of each of these plants as described in three popular vegetation guides and compared to our measured values. To our knowledge, our study is the first to offer relative affinities for the understory species of this region derived empirically from moisture measurements.

We conclude that understory species indicate complex spatial patterns in soil moisture better than any single topographic or edaphic soil moisture proxy for the central Western Cascades. Of the standard proxies that we considered, only elevation was significantly correlated with soil moisture in our study (Table 1). Factors such as soil texture, aspect, and drainage are clearly important components of the water balance, and we have shown elsewhere how these factors can be combined in more sophisticated models to reproduce spatial patterns of soil moisture in the HJA (Lookingbill and Urban 2004). A rapid survey of understory species provides an alternative means of integrating the effects of these multiple influences.

TABLE 3. A comparison of our measured elevation (E) and soil moisture (SM) values (mean values for quadrats containing species) and those given in three commonly used plant identification books: Pojar and McKinnon (1994), Halverson et al. (1986), and Hitchcock and Cronquist (1973).

	Pojar and McKinnon (1994)		Halverson et al. (1986)		Hitchcock and Cronquist (1973)		Measured values	
Species	E	SM	E	SM	E	SM	E (m)	SM (%)
Lower Elevation Species								
Salal	low/mid	n/a	n/a	n/a	lowlnd/lower mtn	dry to moist	753	11.1
Dwarf Oregon grape	low/mid	dry	n/a	n/a	n/a	n/a	1002	11.9
Pacific blackberry	low/mid	dry	n/a	n/a	coast/mid mtn	n/a	1245	13.3
Sword fern	low/mid	moist	all	moist	n/a	moist	968	13.3
Prince's pine	low/mid	n/a	n/a	dry	n/a	n/a	1115	13.6
Twinflower	all	n/a	n/a	n/a	n/a	n/a	969	13.8
Upper Elevation Species								
Oregon bedstraw	all	moist	n/a	n/a	n/a	n/a	1297	12.4
Pathfinder	low/mid	moist	all	moist	n/a	moist	1320	12.9
Beargrass	all	dry	all	dry	sea/montane	dry to moist	1380	13.2
Vine maple	low/mid	moist	n/a	moist	sea/mid mtn	n/a	1112	13.2
Foamflower	low/subalpn	moist	low/montane	moist	up to 1067m	moist	1285	13.8
Wild ginger	low/mid	moist	low/montane	moist	low/montane	moist	1278	14.0
Bunchberry	all	moist	n/a	moist	n/a	moist	1269	14.3
Snowberry	low/mid	dry to moist	low	dry	low/mid mtn	n/a	1259	14.4
Vanilla-leaf	low/mid	moist	low/mid	moist	n/a	moist	1264	14.6
False Solomon's seal	all	moist	low/montane	moist	n/a	moist	1341	16.1
Inside-out-flower	low/mid	moist	low	moist	n/a	moist	1152	16.8

This study focused only on dominant species and did not consider rare/non-dominant species, which may be important constituents of the understory community. To evaluate the potential effect on our ordinations of including more species, we conducted our analyses again using all recorded species and attained results similar to our initial analysis. A larger sampling effort may be required to evaluate more fully the potential of some of these less common plants as indicator species. This would require a more efficient sampling method to reduce the time elapsed between measurements. Even within the relatively short 2-wk period of this study, measurements from permanent dataloggers at the HJA showed a sizable decrease in mean soil moisture (2.3%). This temporal variability points to a major challenge to direct sampling of soil moisture, that the effort required to move across a large landscape will continue to be an obstacle to collecting large soil moisture samples synoptically using a handheld device.

While the measured soil moisture values are representative of this small window of time in mid-summer, the observed patterns in understory species have greater ecological implications. Controls on root zone soil moisture often are not generalizable across time (Grayson and Western 2001). Spatial soil moisture patterns can differ for different seasons for systems characterized by seasonal rainfall (Grayson et al. 1997). Because we are interested in differences in soil moisture as they may affect summer tree growth and because the soils, for the most part, are saturated everywhere during the winter months, we conducted our sampling in July. An advantage of using understory species as moisture indicators is that they integrate soil water levels over time. The patterns that are observed in these species, therefore, should represent patterns in the soil water regime that are important to plants.

We show that understory species are sensitive enough to be used as soil moisture indicators in a predominantly mesic watershed. Vegetation integrates over time and over multiple topographic and edaphic features. Once the general ordering of wet and dry associations and individuals has been determined, a synoptic sample can be collected over a much longer time period than with direct measurements of dynamic soil moisture.

At the HJA, we found that major vegetation community types represent large-scale elevation gradients dominated by temperature variability, but with an underlying moisture trend. Individual species can be used to determine fine-scale moisture differences within a given community type. The observed relationships between vegetation and soil moisture account for the multitude of factors that influence point-specific wetness. To better understand the moisture regime within our forest we should look to these understory plants, otherwise we may trample the wealth of information that lies beneath our feet.

Acknowledgements

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