RELATIONSHIP BETWEEN ENVIRONMENTAL AND VEGETATIONAL PARAMETERS FOR UNDERSTORY AND OPEN-AREA COMMUNITIES

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Abstract.— Ten individuals from each of four tree species were selected, and their associated understory and adjacent open-area communities were sampled for both environmental and vegetational parameters, including light intensity, pH, litter depth, soil depth, and percentages of exposed rock, litter cover, living cover, shrubs, forbs, grasses, and annuals. The four tree species were ponderosa pine, Rocky Mountain juniper, Gambel oak, and snowbrush ceanothus. The study site was in the lower Uinta Mountains about 10 miles east of Kamas, Utah. Correlations among the various biotic and abiotic parameters were examined. The interplay of these factors in differentiating the understory and open-area communities is discussed.

Understanding the relationship of vegetational patterns to environment is a primary goal of community ecology. One aspect of such relationships is the effect of overstory trees and shrubs on their associated understory communities. In a previous report (Wilcox, Brotherson, and Evenson 1981), we examined the influence of four canopy species on their associated understory plant communities in comparison to neighboring communities in open areas outside the canopy influence. The four canopy species were ponderosa pine (*Pinus ponderosa* Dougl.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Gambel oak (*Quercus gambelii* Nutt.), and snowbrush ceanothus (*Ceanothus velutinus* Dougl.).

Many previous studies have reported environmental and vegetational differences between understories and open areas. Light intensity (del Moral 1972, Cline 1966, Blackman 1956) and spectral distribution (Federer and Tanner 1966) are known to strongly differentiate understory and open-area plant communities. Soil moisture and thickness of litter layer are also important factors (Anderson 1969, McQueen 1973), as is soil improvement due to nitrogen fixation by such common understory plants as bitterbrush (*Purshia tridentata* (Pursh) DC.) and snowbrush ceanothus (Wollam and Youngberg 1964, Rusel and Evans 1966, Webster, Youngberg, and Wollam 1967).

Because these and other environmental modifications are influenced by the canopy species, cover (Anderson 1969, McQueen 1973, McConnell and Smith 1970) and diversity (Auclair and Goff 1971) of understory communities are strongly dependent on the canopy tree or large hebaceous species with which they are associated (Gordon 1962, Smith and Cottam 1967).

The present study examines detailed relationships between the various environmental and vegetational parameters measured under the canopies of four tree species and in nearby open areas.

Study Area

The study site is about 10 miles east of Kamas, Utah, along the Yellow Pine branch of Beaver Creek (Fig. 1). This area was chosen because of the homogeneity of the underlying parent material (an alluvial outwash gravel bed) throughout the site, its constant slope and exposure, and its easy accessibility. The study site is an area of "zone jumbling" (Cottam 1930) and contains plant representatives from all life zones except lower sonoran. It is an area of highly mixed vegetation, varying from Douglas fir (*Pseudotsuga men-*

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ziesii (Mirb.) Franco.), white fir (*Abies concolor* Lindl.), and ponderosa pine to clumps of Gambel oak and snowbrush ceanothus. Also interspersed throughout the area are individuals of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Rocky Mountain juniper, quaking aspen (*Populus tremuloides* Michx.), and various other plant species. All can be found at the same elevation and in fairly close proximity.

Because of its apparent uniformity, this site is especially well suited to measure the relationship of environmental and vegetational parameters associated with understories of different tree species and nearby open areas. In such an area, the likelihood of factors other than tree overstory affecting such relationships in a major way is small.

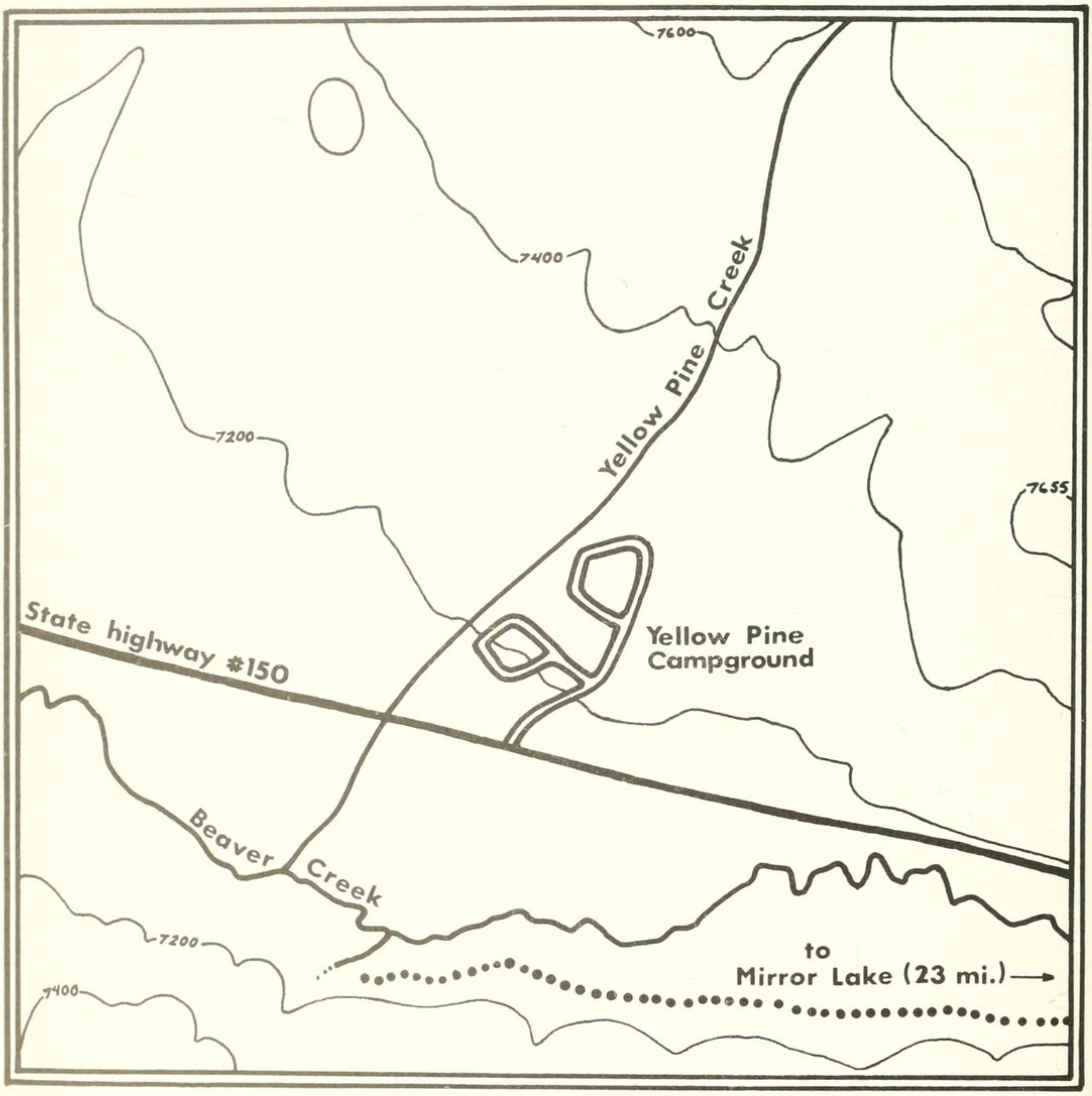
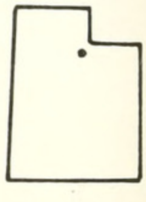


Fig. 1. Map showing location of study site.



METHODS

Ten individuals of each of four tree or shrub species (i.e., ponderosa pine, Rocky Mountain juniper, Gambel oak, and snowbrush ceanothus) were chosen at random in the study area. Eight quadrats (0.25 m^2) were placed around each individual tree or shrub. Four of these quadrats were placed inside the cylinder of the canopy, and four were placed outside the influence of the canopy. To eliminate bias, quadrats were consistently placed one at each direction of the compass. Quadrats were subdivided into four equal units for species frequency measurements. Sample trees and quadrat sites were marked for relocation.

Presence or absence of individual plant species in the understory was determined for all four subunits of each quadrat. All species rooted in the quadrat were recorded. Frequency of each plant species was determined by dividing the number of quadrat subdivisions in which a species occurred by the number of subdivisions sampled. Total living plant cover and composition of plant cover by life form were measured at each quadrat using an ocular estimate method (Daubenmire 1959).

Light intensity was measured in foot-candles at each quadrat, and averages were computed for the understory and open-area quadrats associated with each tree species. All readings were taken between 1200 and 1400 hours on cloud-free days, the last two days of the study.

Soil pH was measured by the colormetric method in the field to avoid pH changes which can occur when soil is stored moist.

Litter depth was measured at the center of all quadrats taken, and soil depth was determined by the average of five penetrometer readings in each quadrat (one at each corner and one in the center). Correlations of all variables with each other were run.

RESULTS AND DISCUSSION

Characteristics of the environment and the vegetation types associated with understory and open-area communities are summarized in Table 1 for the four canopy species. As expected, light intensity values are consistently lower for the understory communities. Understory communities have consistently higher pH (more basic), except for ponderosa pine which shows an understory tending to be slightly more acidic than the open area. Both litter depth and soil depth are far greater in the understory communities than outside the canopies. Percent cover of litter is

TABLE 1. Average measured values of environmental and vegetation parameters for understory and open area communities ± their standard deviations.

	Pinus ponderosa		*Ceanothus velutinus*		*Juniperus scopulorum*		*Quercus gambelii*	
	Understory	Open areas	Understory	Open areas	Understory	Open areas	Understory	Open areas
Light intensity (foot candles)	117 ± 52	225 ± 65	123 ± 29	339 ± 50	168 ± 77	295 ± 67	76 ± 32	242 ± 67
Soil pH	6.3 ± 0.2	6.4 ± 0.1	6.6 ± 0.1	6.4 ± 0.1	7.4 ± 0.6	6.4 ± 0.2	6.6 ± 0.3	6.4 ± 0.2
Litter depth (cm)	6.0 ± 2.7	0.6 ± 0.3	2.1 ± 0.7	0.1 ± 0.1	2.5 ± 0.3	0.3 ± 0.2	2.3 ± 0.6	0.2 ± 0.2
Soil depth (cm)	10.5 ± 2.6	5.3 ± 1.1	6.7 ± 1.7	4.4 ± 1.2	6.1 ± 3.2	4.0 ± 1.6	8.5 ± 2.3	5.7 ± 0.8
% Living cover	20.2 ± 6.0	25.8 ± 6.8	20.0 ± 4.7	31.5 ± 7.6	28.0 ± 19.1	32.0 ± 8.4	27.5 ± 5.2	23.4 ± 5.3
% Litter cover	83.6 ± 6.0	39.0 ± 11.6	45.6 ± 10.0	9.1 ± 7.5	49.3 ± 20.3	13.1 ± 9.0	72.6 ± 5.9	19.3 ± 10.4
% Exposed rock	10.8 ± 5.7	26.3 ± 6.4	24.9 ± 6.8	43.4 ± 11.1	14.8 ± 11.1	32.4 ± 8.1	14.6 ± 9.9	28.5 ± 4.7
% Shrubs	26.8 ± 13.0	27.1 ± 17.0	37.0 ± 16.8	23.9 ± 13.2	48.0 ± 21.9	22.9 ± 17.8	27.7 ± 11.9	18.4 ± 13.6
% Perennial forbs	5.2 ± 7.4	11.4 ± 11.3	18.9 ± 9.7	36.5 ± 12.9	8.0 ± 15.3	31.2 ± 14.9	15.6 ± 9.2	27.4 ± 12.8
% Perennial grasses	11.5 ± 3.4	4.0 ± 3.1	13.9 ± 8.5	7.1 ± 5.9	16.9 ± 13.9	10.4 ± 9.0	22.8 ± 10.2	14.0 ± 9.3
% Annuals	56.6 ± 11.9	57.5 ± 14.5	30.2 ± 12.5	32.4 ± 10.1	27.1 ± 23.9	35.6 ± 25.5	33.9 ± 13.8	40.2 ± 13.1
Average number of species/tree	10.5	11.9	14.2	14.9	10.9	14.3	12.7	14.0
Average number of species/quadrat/tree	4.6	6.2	7.1	6.9	5.4	6.3	7.4	8.4

much greater in the understory, while percent of exposed rock is greater in the open-area communities. Percent living cover is higher in the open-area communities except for oak.

Species preferences for understory and open areas were obtained by taking the difference of total subquadrat occurrences for a species in canopy-covered and open stands and normalizing by dividing by the total occurrences of that species in all stands. The resulting index runs from -1 to 1. Those species with the highest positive values are found most often under the canopy while those species with the greatest negative values are found most often in open areas. Table 2 shows species preference indices and total subquadrat occurrences for each species observed in the study (species are listed alphabetically). Frequency is obtained by dividing the number of occurrences by 160, the total number of subquadrats sampled for each tree species within each type (canopy or open area).

The species preference index was broken down into components relating to each of the four tree species as shown in Table 3. Each component was obtained by taking the difference of the subquadrat occurrences for a species in canopy-covered and open-area stands

TABLE 2. Number of occurrences of each species observed for each of the four canopy species; 160 subquadrats sampled in each category. Life form codes are f = forb, g = grass, c = cool-season or spring ephemeral but perennial (so cf = cool-season forb), sh = shrub, e = evergreen, a = annual, t = tree.

Species	Life form	Preference index	Understory stands				Open-area stands			
			Ceve	Pipo	Jusc	Quga	Ceve	Pipo	Jusc	Quga
Achillea millefolium	f	0.43	3	4	11	32	2	3	9	6
Agoseris glauca	f	-0.31	13	9	3	10	22	23	6	15
Agropyron spicatum	g	0.00	0	0	2	0	0	0	2	0
Agropyron subsecundum	g	0.09	0	2	2	2	0	0	4	1
Agropyron trachycaulum	g	0.56	0	12	2	7	0	0	0	6
Allium acuminatum	cf	-0.30	1	3	3	6	8	9	6	1
Amelanchier alnifolia	sh	-0.50	0	1	0	0	0	1	2	0
Antennaria luzuloides	f	1.00	0	0	0	1	0	0	0	0
Antennaria rosea	f	-1.00	0	0	0	0	0	0	1	0
Apocynum androsaemifolium	f	-0.78	2	0	0	0	9	7	0	0
Arctostaphylos uva-ursi	esh	1.00	0	0	4	0	0	0	0	0
Artemisia tridentata	esh	-1.00	0	0	0	0	0	0	1	0
Aster chilensis var. adscendens	f	-0.28	6	0	0	3	10	0	0	6
Bromus ciliatus	g	0.32	11	11	4	9	2	5	6	5
Bromus tectorum	g	-1.00	0	0	0	0	0	0	0	1
Carex geyeri	eg	0.36	6	9	35	43	1	15	22	6
Carex rossii	eg	0.31	23	0	1	18	14	0	7	1
Ceanothus velutinus	esh	0.09	0	0	6	0	0	0	5	0
Chenopodium ambrosioides	a	1.00	0	0	0	3	0	0	0	0
Chenopodium fremontii	a	-0.32	9	1	0	5	20	0	3	6
Chrysopsis villosa	f	-0.79	8	0	4	0	33	17	42	10
Cirsium undulatum	f	-0.33	1	0	0	0	0	0	2	0
Collinsia parviflora	a	-0.13	7	33	39	19	18	41	36	33
Collomia linearis	a	-0.19	20	35	36	28	33	66	39	37
Comandra umbellata	cf	0.07	11	2	4	5	8	1	8	2
Cryptantha circumscissa	a	-0.42	6	1	0	0	16	0	0	1
Eriogonum heracleoides	esh	0.07	1	14	7	0	1	0	9	9
Erysimum asperum	f	-1.00	0	0	0	0	1	0	0	0
Euphorbia robusta	f	1.00	1	0	0	0	0	0	0	0
Galium boreale	f	-1.00	0	0	0	0	0	0	0	1
Gayophytum ramosissimum	a	-0.91	1	2	1	1	11	5	30	59
Hydrophyllum capitatum	cf	-0.02	4	1	5	10	2	5	4	10
Ipompsis aggregata	f	-1.00	0	0	0	0	0	1	0	0
Juniperus communis	esh	1.00	0	0	4	0	0	0	0	0
Lomatium grayi	f	-0.05	7	9	2	0	15	2	3	0
Mahonia repens	esh	0.08	70	40	60	48	47	43	44	50

associated with one of the four canopy species. This difference was then normalized by dividing by the total occurrence of that species in all stands. The four components thus sum to the species preference index discussed above (within round-off error). The components of the species preference index clarify how a species preference for understories or open areas is associated with a particular canopy species. Some understory species are highly associated with a particular canopy tree species, and others are not. For example, *Carex geyeri*'s preference for the understory is strongly associated with Gambel oak. Yet, *Stellaria jamesiana* prefers the understory much more evenly for three of the four canopy species.

Correlation analysis was performed to study the relationship of the environmental and vegetational parameters which were measured. Table 4 shows the significant positive and negative correlations.

Light intensity correlates significantly with all variables except percent annuals. The negative correlation of light intensity with pH, litter depth, soil depth, and percent litter cover is to be expected because of the generally higher values of these parameters under the canopies. Similarly, there is more exposed rock and living cover in the open areas. The correlations of light intensity with life forms reflect the preference of shrubs and grasses for understory areas and forbs and annuals for open areas (Wilcox, Brotherson, and Evenson 1981).

The significant correlations of pH with

TABLE 2 continued.

Species	Life form	Preference index	Understory stands				Open-area stands			
			Ceve	Pipo	Jusc	Quga	Ceve	Pipo	Jusc	Quga
Melica bulbosa	g	1.00	0	2	0	0	0	0	0	0
Mertensia brevistyle	f	-1.00	0	0	0	0	2	0	0	0
Osmorhiza obtusa	f	-1.00	0	0	0	0	0	0	0	1
Pachystima myrsinites	esh	0.19	3	2	10	4	2	3	6	2
Penstemon sp.	f	-1.00	0	0	0	0	0	0	2	0
Pinus contorta	et	1.00	0	0	0	1	0	0	0	0
Pinus ponderosa	et	0.00	0	1	0	0	0	1	0	0
Poa curta	g	-0.36	0	0	0	7	0	0	3	12
Poa fendleriana	g	-1.00	0	0	0	0	3	0	0	0
Poa pratensis	g	0.11	0	5	0	0	0	0	4	0
Polygonum douglasii	a	-0.51	65	17	29	28	129	92	87	119
Potentilla glandulosa	f	-0.11	3	0	0	1	0	0	1	4
Prunus virginiana	sh	0.54	1	1	6	2	0	2	1	0
Purshia tridentata	sh	1.00	1	0	0	1	0	0	0	0
Quercus gambelii	t	1.00	0	0	1	0	0	0	0	0
Rosa woodsii	sh	0.20	5	5	6	8	6	4	2	4
Sedum stenopetalum	f	-0.36	6	4	15	3	20	11	21	7
Senecio uintahensis	f	-0.64	2	0	0	0	4	0	1	4
Silene menziesii	ef	0.33	0	2	0	0	1	0	0	0
Solidago missouriensis	f	-0.69	5	2	1	0	25	9	9	0
Solidago multiradiata	f	0.05	9	17	4	2	4	17	6	2
Solidago sparsiflora	f	-0.53	0	0	0	11	0	13	0	23
Stellaria jamesiana	cf	0.51	55	94	27	105	11	36	16	27
Stipa columbiana	g	-1.00	0	0	0	0	0	0	0	5
Stipa lettermanii	g	0.09	5	1	5	1	5	3	2	0
Symphoricarpos oreophilus	sh	0.20	8	2	12	5	4	3	9	2
Taraxacum officinale	f	0.00	4	6	2	2	2	4	3	5
Thalictrum fendleri	f	1.00	0	0	6	0	0	0	0	0
Thlaspi montanum	f	-0.20	53	16	28	40	48	55	25	76
Tragopogon dubius	a	0.25	5	0	0	0	1	0	2	0
Viguiera multiflora	f	0.00	9	0	2	2	5	6	0	2
Viola nuttallii	cf	0.00	0	0	0	1	0	0	0	1
Viola purpurea	f	0.52	11	0	0	5	1	2	0	2
Total number of species			39	34	36	37	38	32	41	39

other variables again reflect the tendency toward higher pH under the canopies. Similarly, for litter depth, soil depth, percent exposed rock, percent litter cover, and percent living cover the correlations generally reflect the relationship of these parameters to the canopy-covered or open-area condition.

Correlations of these parameters with percent annuals are not so easily interpreted, however. Annuals tend slightly to prefer the open areas, hence the negative correlation with pH. Their positive correlation with percent litter cover, however, is better understood by observing the negative correlation with all other life forms and percent living cover. Annuals tend to grow in annual-dominated communities with relatively low total living cover and significant amounts of litter cover.

By contrast, shrubs and forbs are positively correlated with percent living cover, but negatively correlated with each other. Shrubs provided a significant proportion of living cover in any quadrat in which they occur just because of their size. This fact accounts for their positive correlation with living cover. However, shrubs tend to prefer understory habitats and forbs prefer the open areas. So forbs are positively correlated with living cover due to the greater cover outside the canopies, while being negatively correlated with shrubs.

TABLE 3. Preference index components by tree species. Life form codes are as in Table 2.

Species	Life form	Preference index	Preference index components			
			Ceve	Pipo	Jusc	Quga
Antennaria luzuloides	f	1.00	0.00	0.00	0.00	1.00
Arctostaphylos uva-ursi	esh	1.00	0.00	0.00	1.00	0.00
Chenopodium ambrosioides	a	1.00	0.00	0.00	0.00	1.00
Euphorbia robusta	f	1.00	1.00	0.00	0.00	0.00
Juniperus communis	esh	1.00	0.00	0.00	1.00	0.00
Melica bulbosa	g	1.00	0.00	1.00	0.00	0.00
Pinus contorta	et	1.00	0.00	0.00	0.00	1.00
Purshia tridentata	sh	1.00	0.50	0.00	0.00	0.50
Quercus gambelii	t	1.00	0.00	0.00	1.00	0.00
Thalictrum fendleri	f	1.00	0.00	0.00	1.00	0.00
Agropyron trachycaulum	g	0.56	0.00	0.44	0.07	0.04
Prunus virginiana	sh	0.54	0.08	-0.08	0.38	0.15
Viola purpurea	f	0.52	0.48	-0.10	0.00	0.14
Stellaria jamesiana	cf	0.51	0.12	0.16	0.03	0.21
Achillea millefolium	f	0.43	0.01	0.01	0.03	0.37
Carex geyeri	eg	0.36	0.04	-0.04	0.09	0.27
Silene menziesii	ef	0.33	-0.33	0.67	0.00	0.00
Bromus ciliatus	g	0.32	0.17	0.11	-0.04	0.08
Carex rossii	eg	0.31	0.14	0.00	-0.09	0.27
Tragopogon dubius	a	0.25	0.50	0.00	-0.25	0.00
Rosa woodsii	sh	0.20	-0.02	0.02	0.10	0.10
Symphoricarpos oreophilus	sh	0.20	0.09	-0.02	0.07	0.07
Pachystima myrsinites	esh	0.19	0.03	-0.03	0.12	0.06
Poa pratensis	g	0.11	0.00	0.56	-0.44	0.00
Agropyron subsecundum	g	0.09	0.00	0.18	-0.18	0.09
Ceanothus velutinus	esh	0.09	0.00	0.00	0.09	0.00
Stipa lettermanii	g	0.09	0.00	-0.09	0.14	0.05
Mahonia repens	esh	0.08	0.06	-0.01	0.04	-0.00
Comandra umbellata	ef	0.07	0.07	0.02	-0.10	0.07
Eriogonum heracleoides	esh	0.07	0.00	0.34	-0.05	-0.22
Solidago multiradiata	f	0.05	0.08	0.00	-0.03	0.00
Agropyron spicatum	g	0.00	0.00	0.00	0.00	0.00
Pinus ponderosa	et	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	f	0.00	0.07	0.07	-0.04	-0.11
Viguiera multiflora	f	0.00	0.15	-0.23	0.08	0.00

Summary and Conclusions

Canopy tree species clearly influence both vegetation and environment in their understories (Wilcox, Brotherson, and Evenson 1981). The effects of this influence on plant distributions are shown clearly for individual species in Tables 2 and 3.

The correlations of the environmental and vegetational parameters among themselves can be understood on the basis of a few important concepts.

(1) The environmental parameters (light intensity, pH, litter depth, soil depth, percentage of exposed rock, and percentage of litter cover) are directly influenced by the presence or absence of canopy cover. All correlations among these parameters are as expected on that basis.

(2) The vegetational correlations follow primarily from the facts that there is more living cover in open areas than in the understories; shrubs and grasses tend to prefer the understories; and forbs and annuals tend to prefer open areas.

(3) Shrubs follow the pattern inferred from their tendency to prefer understory areas except for their positive correlation with the percentage of living cover. This is because shrubs themselves provide a large fraction of the living cover that is found in understory quadrats.

(4) Annuals are different. They apparently tend to grow in annual-dominated patches with low total living cover and relatively high litter cover.

Table 3 continued.

Species	Life form	Preference index	Preference index components			
			Ceve	Pipo	Jusc	Quga
Viola nuttallii	cf	0.00	0.00	0.00	0.00	0.00
Hydrophyllum capitatum	cf	-0.02	0.05	-0.10	0.02	0.00
Lomatium grayi	f	-0.05	-0.21	0.18	-0.03	0.00
Potentilla glandulosa	f	-0.11	0.33	0.00	-0.11	-0.33
Collinsia parviflora	a	-0.13	-0.05	-0.04	0.01	-0.06
Collomia linearis	a	-0.19	-0.04	-0.11	-0.01	-0.03
Thlaspi montanum	f	-0.20	0.01	-0.11	0.01	-0.11
Aster chilensis var. adscendens	f	-0.28	-0.16	0.00	0.00	-0.12
Allium acuminatum	cf	-0.30	-0.19	-0.16	-0.08	0.14
Agoseris glauca	f	-0.31	-0.09	-0.14	-0.03	-0.05
Chenopodium fremontii	a	-0.32	-0.25	0.02	-0.07	-0.02
Cirsium undulatum	f	-0.33	0.33	0.00	-0.67	0.00
Poa curta	g	-0.36	0.00	0.00	-0.14	-0.23
Sedum stenopetalum	f	-0.36	-0.16	-0.08	-0.07	-0.05
Cryptantha circumscissa	a	-0.42	-0.42	0.04	0.00	-0.04
Amelanchier alnifolia	sh	-0.50	0.00	0.00	-0.50	0.00
Polygonum douglasii	a	-0.51	-0.11	-0.13	-0.10	-0.16
Solidago sparsiflora	f	-0.53	0.00	-0.28	0.00	-0.26
Senecio uintahensis	f	-0.64	-0.18	0.00	-0.09	-0.36
Solidago missouriensis	f	-0.69	-0.39	-0.14	-0.16	0.00
Apocynum androsaemifolium	f	-0.78	-0.39	-0.39	0.00	0.00
Chrysopsis villosa	f	-0.79	-0.22	-0.15	-0.33	-0.09
Gayophytum ramosissimum	a	-0.91	-0.09	-0.03	-0.26	-0.53
Antennaria rosea	f	-1.00	0.00	0.00	-1.00	0.00
Artemisia tridentata	esh	-1.00	0.00	0.00	-1.00	0.00
Bromus tectorum	g	-1.00	0.00	0.00	0.00	-1.00
Erysimum asperum	f	-1.00	-1.00	0.00	0.00	0.00
Galium boreale	f	-1.00	0.00	0.00	0.00	-1.00
Ipompsis aggregata	f	-1.00	0.00	-1.00	0.00	0.00
Mertensia brevistyla	f	-1.00	-1.00	0.00	0.00	0.00
Osmorhiza obtusa	f	-1.00	0.00	0.00	0.00	-1.00
Penstemon sp.	f	-1.00	0.00	0.00	-1.00	0.00
Poa fendleriana	g	-1.00	-1.00	0.00	0.00	0.00
Stipa columbiana	g	-1.00	0.00	0.00	0.00	-1.00

TABLE 4. Significance levels for correlations of life form types, cover, and measured environmental parameters for all stands studied.

Variables	2	3	4	5	6	7	8	9	10	11
1. Light intensity	-.1	-.001	-.001	+.001	-.001	+.1	-.05	+.001	-.001	NS
2. pH		NS	NS	-.05	NS	NS	+.05	-.01	NS	-.05
3. Litter depth			+.001	-.001	+.001	NS	+.1	-.001	NS	NS
4. Soil depth				-.001	+.001	-.05	NS	-.01	+.1	NS
5. % exposed rock					-.001	+.1	-.1	+.001	-.01	NS
6. % litter cover						-.001	NS	-.001	+.001	+.05
7. % living cover							+.01	+.1	NS	-.001
8. % shrubs								-.001	NS	-.001
9. % forbs									NS	-.05
10. % grasses									NS	-.05
11. % annuals										
										-.01

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