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PRODUCTIVITY OF THE UNDERSTORY COMMUNITY
IN AN ARIZONA PONDEROSA PINE FOREST.

THE UNIVERSITY OF ARIZONA, PH.D., 1978

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PRODUCTIVITY OF THE UNDERSTORY COMMUNITY
IN AN ARIZONA PONDEROSA PINE FOREST

by

Steven Paul McLaughlin

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF GENERAL BIOLOGY

In Partial Fulfillment of the Requirements .
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN BOTANY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 7 8

THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my
direction by Steven Paul McLaughlin

entitled Productivity of the Understory Community in an Arizona
Ponderosa Pine Forest

be accepted as fulfilling the dissertation requirement for the
degree of Doctor of Philosophy

Willard Van Dsdale
Dissertation Director

June 10, 1978
Date

As members of the Final Examination Committee, we certify
that we have read this dissertation and agree that it may be
presented for final defense.

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June 10, 1978
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Final approval and acceptance of this dissertation is contingent
on the candidate's adequate performance and defense thereof at the
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SIGNED: Steven Paul McLaughlin

PREFACE

I would like to briefly explain the rationale for the organization of this dissertation. It was my intention to write in the concise, organized style of modern scientific publications. The work presented herein, like most dissertations, is a compilation of several complementary studies. I have elected to present them independently in the format of a main body and several supporting appendices. The appendices are condensations of separate manuscripts and reports, edited to remove redundant material.

I was supported during the course of this dissertation research by USDA Forest Service Cooperative Agreement No. 16-512-CA to the School of Renewable Natural Resources, a grant from the ANAMAX Mining Company to the Department of General Biology, and Graduate Teaching Assistantships from the Department of General Biology. Completion of this dissertation was facilitated by the help and cooperation of several faculty members: Dr. Willard Van Asdall provided encouragement and valuable discussion throughout my graduate study, in addition to making his home available for the typing of the dissertation; Dr. Robert F. Wagle provided field accommodations and vehicles and other technical assistance; Dr. J. O. Klemmedson provided his laboratory for weighing plant materials; Dr. T. Curtis Tucker provided access to and assistance with the atomic absorption spectrophotometer; and Dr. Annita Harlan consented to substitute on the committee at the eleventh hour. All of the above provided invaluable technical review and criticism. Discussions

with graduate student colleagues was a particularly valuable source of help, criticism, and review--I would like to especially acknowledge Thomas Eakle, Brad Musick, and Martin Karpiscak. Doug McAda and Lisa Haynes provided competent assistance in the field at the typically low rates of pay undergraduates receive.

I would finally like to dedicate this dissertation to my parents, Winfred and Gloria McLaughlin, for their help and encouragement throughout my education.

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ABSTRACT

Studies were conducted in an Arizona ponderosa pine forest to determine the production of the understory community, its seasonal distribution, and the most important influences of the pine stand in controlling its spatial distribution.

Net annual primary production of the understory was estimated at 568 kg/ha/yr, distributed as follows: grasses and sedges, 230 kg/ha/yr; composites, 86 kg/ha/yr; legumes, 127 kg/ha/yr; other herbs, 77 kg/ha/yr; and Pteridium aquilinum, 49 kg/ha/yr. Total understory plants showed a biseasonal pattern of production, with legumes reaching a peak in production in spring, other herbs in mid-summer, and grasses and sedges and composites in late-summer.

Eighty-one species were encountered in the sampling for understory plants, and their production values were distributed in a log-normal manner. Most species were rare in occurrence--only eight were found in 20% or more of the quadrats.

The major influences of the overstory on understory production were associated with soil potassium, light reduction below the canopy, and stand age. Since soil potassium was directly correlated with overhead canopy cover and litter attributes, it seems likely that pine trees determined the distribution of potassium in the upper soil horizons through leaching of the canopy and litterfall. High soil potassium appeared to be inhibitory to many understory taxa. The influence of

stand age may be attributed to higher soil fertility in young stands or to grazing patterns of cattle, since many species were more abundant in the young, dense, less accessible stands of small trees.

Overall, the understory species demonstrated a complex pattern of niche-differentiation with respect to overstory, litter, soils, and seasonality. The spatial heterogeneity in stand structure and the seasonal heterogeneity in rainfall that characterize this ponderosa pine forest probably account for the high species diversity in the understory community.

INTRODUCTION

Ecological studies of forest communities in the United States have emphasized the overstory while largely ignoring the understory. Historical and practical factors have contributed to this emphasis on the overstory. American plant ecologists always have had a diversity of natural forest stands available for study. Important theoretical advances, such as the continuum (Curtis and McIntosh 1951), and technical advances, such as gradient analysis (Whittaker 1956) and ordination (Bray and Curtis 1957), developed from studies of forest overstory communities. In contrast, at the time plant ecology developed as a science in the nineteenth century, most European forests were intensively managed plantations. Since characteristics of the overstory, such as species composition, distribution, and abundance were determined by management practices, European phytosociologists concentrated on the classification and distribution of the more variable, unmanaged ground vegetation.

Within a forest stand, trees constitute most of the biomass and are the easiest life form to work with. Measures of tree abundance such as basal area and density are easily determined. There are relatively few species of trees in temperate forest ecosystems and tree species are not difficult to identify at any time of the year. In contrast, the herbaceous understory community may contain numerous species, many of which may be rare and highly variable in their

distribution. Density is difficult to determine and probably is not a useful parameter for many understory plants because of their small but variable size, diversity of growth forms, and pronounced tendency to reproduce vegetatively (Tumidajowicz 1975, 1977). Biomass or production¹ are more realistic measures of an understory species' importance in the community, since these parameters are better indicators of the species' use of environmental resources, adaptation to the physical environment, and competitive ability. However, the sampling required to estimate biomass and production is intensive and time-consuming.

The factors controlling the distribution and production of understory species within a forest are not well understood. Since canopy trees intercept light and precipitation and compete for soil moisture and nutrients, the production of understory plants is generally thought to be inversely related to the overstory cover (Anderson, Loucks, and Swain 1969; Siccama, Bormann, and Likens 1970). In the eastern deciduous forests, understory production is highest in the spring before the canopy foliage develops (Bazzaz and Bliss 1971). However, other important factors in addition to light influence the distribution of understory species in deciduous forests, such as microtopography (Bratton 1976a), soil depth (Bratton 1976b), topography and "tip-ups" (Struick and Curtis 1962), and elevation above the stream channel (Bell 1974).

1. Biomass refers to the standing crop present at a particular time and is expressed in this study in units of kg/ha. Production, as used herein, refers to the yield or total biomass produced during the growing season and is expressed in units of kg/ha/yr. Productivity refers to the rate of biomass accumulation, expressed herein in units of kg/ha/day.

In western ponderosa pine forests, most of the work on understory plants has concentrated on demonstrating that understory cover or production decreases as the abundance of pine increases. Decreases in understory production have been related to increases in pine canopy coverage (Arnold 1950; Pase 1958; Cooper 1960b; McConnell and Smith 1965, 1970; Clary 1969; Clary, Kruse, and Larson 1975), basal area (McConnell and Smith 1965; Reynolds 1969; Clary 1969; Clary, Kruse, and Larson 1975; Ffolliott and Clary 1975), and production (Ffolliott and Clary 1974). Despite the repeated demonstration of these relationships, the actual ecological mechanisms have not been identified. Variation in ponderosa pine stand structure can alter the understory environment in at least nine potentially significant ways, by: (1) decreasing the amount of light reaching the forest floor (Moir 1966); (2) decreasing the amount of precipitation reaching the forest floor (Helvey 1974); (3) withdrawing soil water and nutrients; (4) building up the forest floor through litterfall; (5) reducing soil pH (Zinke 1962); (6) reducing nitrification rates (Moir 1966); (7) increasing the levels of nutrient cations in the soil (Zinke 1962); (8) maintaining a high C/N ratio (Moir 1966); and (9) altering the microclimate.

Little work has been done to evaluate the relative importance of the above overstory influences on understory vegetation. Reynolds (1969) showed that the relationship between herbage production and ponderosa pine basal area is different in stands of immature and mature trees, implying that the size or age of trees influences the understory. Pase (1958), Clary, Ffolliott, and Jameson (1968), and Biswell (1973) have shown that the amount of litter buildup is correlated to

understory production, and Moir (1966) suggested that both light reduction and reduced nitrification under a dense stand contribute to lowered herbage production. Working in stands of white pine and red pine in northern Wisconsin, Anderson et al. (1969) showed that differences in throughfall precipitation may be more significant to the understory than differences in light levels below the canopy. No studies comparable to that of Anderson et al. have been conducted in ponderosa pine forests.

The objectives of this study are to determine: (1) the production of the understory community, (2) how that production is distributed throughout the growing season and among the component species, and (3) how various attributes of the pine stand influence that production. The author hopes that the results reported herein will be a significant contribution to the understanding of the ecology of forest understory communities.

STUDY SITE

Location

The study site is located in the White Mountains, five miles northeast of McNary in Apache County, Arizona, on the Fort Apache Indian Reservation along its northern boundary with Apache-Sitgraves National Forest. Elevation is about 2350 m. Topography is generally level with scattered cinder cones.

Geology, Soils, and Climate

The substrate throughout the McNary area is a Quaternary basalt (Wilson, Moore, and O'Haire 1960). Forested soils derived from this basalt have silt loam textured topsoils and clay loam textured B horizons (Boul 1966). On the study site, soils are typic argiborolls mapped as Sponsellor gravelly silt loams and Broliar cobly silt loams (Bureau of Indian Affairs, personal communication).

Climatic data are available in Green and Sellers (1964) for McNary (Figure 1). The mean annual precipitation of 627 mm is biseasonal in distribution with storms of cyclonic origin bringing rain and snow from December through March. Summer precipitation is of convective origin and occurs primarily from July through September. Mean minimum monthly temperatures are above freezing from May to October. The water year October 1975 through September 1976, when data on understory plants was collected, had precipitation below normal in early winter and above normal in late winter, but temperature and total precipitation during

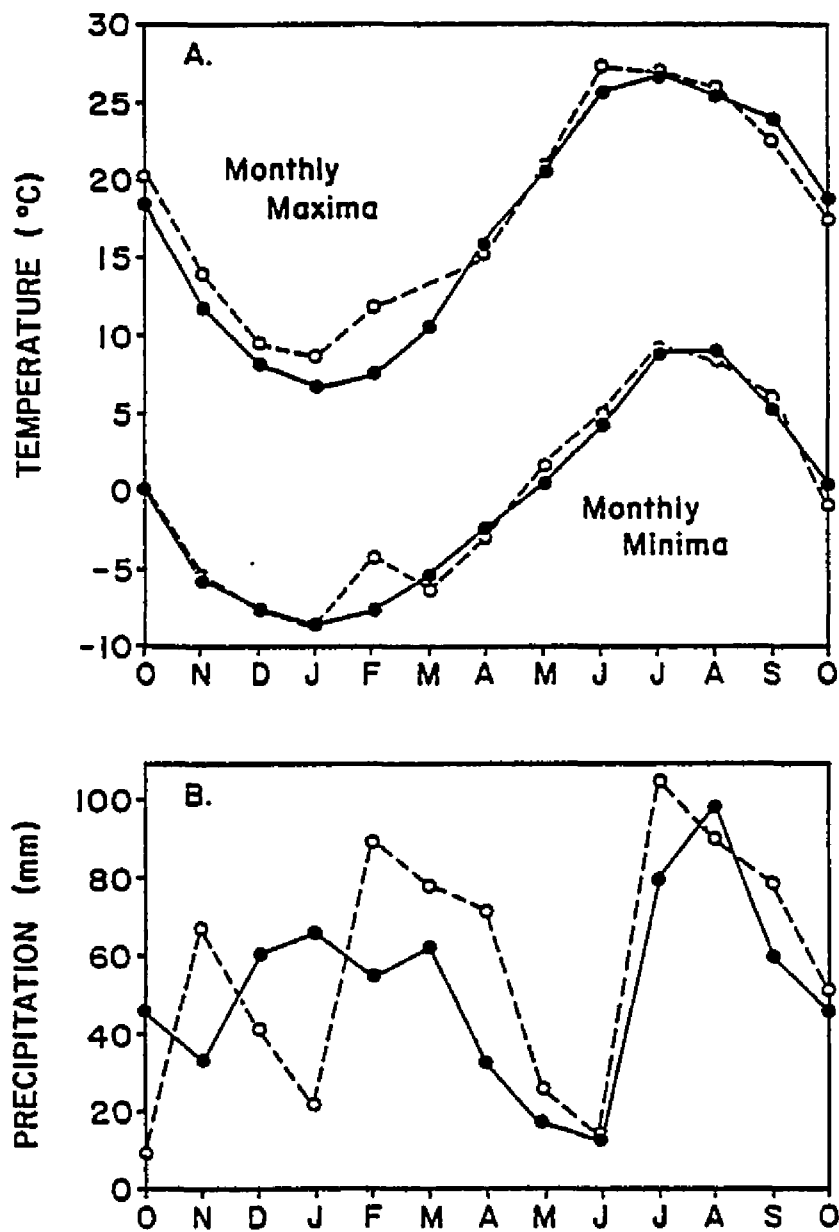


Figure 1. Climate at McNary, Arizona. -- Temperature (A) and precipitation (B). Solid lines are for long-term averages, dashed lines are for the water year October 1975 through September 1976.

the growing season near normal with a warmer than average period in mid-winter (Figure 1).

Flora

The vascular flora on the study site is listed in Appendix A. This flora was compiled from collections made by the author from 1974 to 1977. Voucher specimens are deposited in the University of Arizona Herbarium. The flora is composed of 180 species, distributed among 128 genera in 42 families. The overstory is dominated by ponderosa pine (Pinus ponderosa), with scattered stands of aspen (Populus tremuloides), locust (Robinia neomexicana), and oak (Quercus gambelii) and isolated individuals of white pine (Pinus strobiformis) and Douglas fir (Pseudotsuga menziesii). The understory contains only two shrubs (Rosa arizonica and Ceanothus fendleri) and a herbaceous flora rich in members of the Compositae (41 species), Gramineae (27 species), Leguminosae (14 species), Scrophulariaceae (9 species), and Cyperaceae (8 species). Genera with four or more species are Erigeron (7), Carex (6), Senecio (4), Muhlenbergia (4), and Polygonum (4). The collections were all obtained from a topographically homogeneous locale with a total area of only 0.5 km², yet they represent approximately 5% of the flora of the entire state of Arizona, indicating that the community is floristically very diverse.

METHODS

All data were gathered along 20 pairs of permanently established plots. Plot size was 30 m by 2.7 m (81 m²). Fifteen of the plot pairs were in pine stands, three were in aspen stands, and two were in locust stands. Undisturbed ponderosa pine forests in the Southwest have characteristically patchy structures, generally composed of numerous, small, even-aged stands (Cooper 1960a). Within a stand the pattern of tree distribution is usually random (Cooper 1961). Such a pattern was evident on the study site, and individual plots were situated within the approximate boundaries of single, even-aged stands. Plots were paired on the basis of similarity in stand structure and the plot pairs were established subjectively in a wide range of stands in an effort to include as much variation in stand structure as possible. One long edge of each plot was predesignated as a transect for sampling overstory attributes, litter, soil, and understory plants.

Environmental Attributes

Canopy cover is a general term including many attributes of the canopy structure of possible importance to understory plants. Transmissivity, referring to the permeability of the canopy to light, was measured with a spherical densiometer (Lemmon 1956) by taking readings in the east, south, and west directions at nine randomly selected points per plot. This method of quantifying the canopy structure gave an estimate of transmissivity directly proportional to light penetration

(Appendix B). At the same nine sample points, overhead canopy cover was determined from canopy photographs taken with a 50 mm lens. This method of quantifying the canopy structure gave a measure inversely proportional to the amount of throughfall (Appendix B).

Other stand attributes measured included tree basal area, density, and canopy height. A 1:25 angle-gauge was used to measure basal area at the same nine points used to measure canopy cover attributes. Density was determined by counting all living trees within the plot with a diameter breast height (d.b.h.) greater than 5 cm. Canopy height was the average height of all trees within the plot with a d.b.h. greater than 5 cm. Tree height was determined with an inclinometer.

The forest floor was removed from six randomly selected quadrats per plot located along the predesignated plot edge. Quadrats measured 53 cm by 56 cm. An effort was made to separate the O1 (litter) layer from the O2 (duff) layer in the field, but the separations appeared to be arbitrary and inconsistent. The samples were bagged and returned to the lab at McNary for sieving through a hardware cloth (5 mm) mesh. The fraction retained by the sieve was designated the O1 layer, and the fraction passing through the sieve was designated the O2 layer. This technique appeared to give a reasonable and repeatable separation of the O1 and O2 layers. Litterfall was measured over a two year period in three 13.9 dm^2 litter boxes per plot. All litter samples were air-dried for one month and weighed to the nearest 0.1 gm.

Surface rock cover was determined by the point-quadrat method with a sample size of 1800 points per plot. Soil samples from the top 0-5 cm of the A1 horizon were collected after removing the litter from

six quadrats per plot. Samples were analyzed for total nitrogen, nitrate, phosphate, organic matter, and pH by the Soil, Water, and Plant Testing Laboratory at The University of Arizona. Calcium and magnesium were determined by atomic absorption, and potassium and sodium were determined by flame emission. Percentage sand and clay were determined by hydrometer analysis.

Understory Plants

On each of six sampling dates spaced at 4-week intervals during the 1976 growing season, biomass was measured by clipping all above-ground understory vegetation in three quadrats per plot, each 53 cm by 56 cm. Quadrat locations were randomly selected along the predesignated edge of each plot, with the restrictions that one quadrat was located along each one-third (10 m by 2.7 m) of the plot and that no quadrat was clipped more than once. All quadrats were enclosed in portable exclusion cages to prevent grazing of sample locations by cattle or elk. Clippings were separated by species, air-dried for three weeks, and weighed to the nearest .01 gm. Production was calculated separately for each plot from the biomass data using the method of summation of positive increments (Kelly, Van Dyne, and Harris 1974; Appendix C).

Data on cover and frequency of understory plants also are included in this study. Frequency data were extracted from the 540 clipped quadrats in pine stands (30 plots x 3 quadrats/plot/date x 6 dates). Cover was determined by the point-quadrat method (Goodall 1952) with a sample of 900 points per plot. Sampling for cover was conducted from 15 June to 19 June, 1976.

Data Analysis

All data were analyzed using computer programs discussed and documented in Nie et al. (1975). Since the statistical procedures used assume that the independent variables are normally distributed, log transformations were applied to the production data. This transformation appeared to result in sampling distributions more closely approximating normal distributions for all understory taxa examined. The transformation used was $\log(Y + 1)$, where Y was the net annual primary production in kg/ha/yr.

Relationships among environmental (overstory, litter, and soil) attributes were analyzed using Pearson product-moment correlation coefficients. Relationships between understory taxa and environmental attributes were analyzed using Pearson product-moment correlation coefficients and stepwise multiple regression. Regression analysis is used herein to determine the independent influence of each environmental attribute on each understory taxon investigated, rather than to derive models for predicting understory production. An objective of this study was to determine the relative importance of overstory, litter, and soil influences on understory production, and stepwise multiple regression is an appropriate tool to accomplish this objective. The first independent variable selected for inclusion in a stepwise regression equation is the one with the highest simple correlation with the dependent variable. Thereafter, partial correlations are computed at each subsequent step between the residuals and the remaining independent variables, and the independent variable with the highest absolute partial correlation is selected for inclusion. Thus the R^2

(coefficient of determination) change at each step provides a measure of the independent variable's influence after adjusting for the variance accounted for by prior, more influential variables.

Data reported in this dissertation were gathered during a study of the effects of prescribed burning on canopy, litter, soils, and understory production. The results of that study are discussed in Appendix D. Since the only statistically significant effect of the burn was a slight reduction in the O₁ litter on the burn plots, data from burn and control plots were pooled for the analysis and discussion of overstory/understory relationships. Preburn estimates of O₁ litter were used in the analyses.

Only data from the plot pairs in pine stands were used herein. While interesting differences and patterns were observed on the locust and aspen plots, the number of plots in these deciduous types was too few for statistical comparison and analysis.

RESULTS AND DISCUSSION

Environmental Attributes

Descriptive statistics for the overstory, litter, and soil attributes measured on the fifteen plot pairs in ponderosa pine stands are listed in Table 1. Of the stand attributes, the plots were most variable in density and canopy height. The ranges of overhead canopy cover and basal area correspond to conditions of moderately open to very dense ponderosa pine stands in this area. Total litter on the plots averaged 25 tons/ha with an annual litterfall of 1.42 tons/ha/yr. Variation in litterfall and litter accumulations was slightly greater than the variation in overhead canopy cover, transmissivity, and basal area. The amount of surface rock was highly variable. Topsoils were generally fine textured, varying from loams to clay loams. Variation in pH was notably low. The soils averaged 8.7% organic matter with an average C/N ratio of 18.3. Calcium, magnesium, and potassium levels were high; phosphate was low.

Understory Plants

Cover, frequency, and production data on the 81 understory species recorded in the samples from pine plots are listed in Table 2. Total cover in June was 19.0%, with one species, Trifolium rusbyi, accounting for over one-third (7.0%) of this total. Only four other species had a cover of 1% or more: Poa pratensis (2.1%), Sitanion

Table 1. Descriptive statistics for environmental attributes on pine plots.

Attribute	Units	Mean	Range	C.V. (%) ^a
Overstory Attributes				
Transmissivity	% open	36.7	23.5-51.4	18.7
Overhead canopy cover	% closed	43.7	27.2-60.6	17.8
Canopy height	meters	11.5	5.5-25.0	53.6
Density	number/ha	2076	247-5313	63.4
Basal area	m ² /ha	43.3	23.1-63.1	19.8
Litter Attributes				
01 litter layer	tons/ha	10.35	5.5-17.5	28.8
02 litter layer	tons/ha	14.77	7.4-24.2	27.2
Litterfall	tons/ha/yr	1.42	.83-2.31	23.8
Soil Attributes^b				
Surface rock	% coverage	2.15	0-16.3	164.7
Organic matter	per cent	8.69	4.5-14.0	27.3
Total nitrogen	ppm	2751	1716-4410	23.1
pH	$-\log_{10} \text{H}^+$	5.8	5.5-6.2	2.4
Nitrate	ppm	16.5	10.7-29.2	28.4
Phosphate	ppm	2.62	1.3-4.8	40.8
Calcium	meq/100 gm	8.83	6.74-11.65	15.8
Magnesium	meq/100 gm	5.80	3.44-8.70	21.7
Sodium	meq/100 gm	.21	.15-.30	19.5
Potassium	meq/100 gm	1.26	.76-2.78	39.7
Sand	per cent	33.6	23.7-42.8	13.9
Clay	per cent	28.2	22.6-36.9	12.9

^aCoefficient of variation

^bAnalysis performed on less than 2 mm fraction

Table 2. Understory cover, frequency, and production on ponderosa pine plots.

Taxon	Cover (%)	Freq. ^a (%)	Production (kg/ha/yr)		
			Spr/ES ^b	LS/Fall ^c	NAPP ^d
<u>Agrostis scabra</u>	.03	3.9	1.36	.44	1.80
<u>Blepharoneuron tricholepis</u>	.01	2.6	.49	.55	1.04
<u>Bromus porteri</u>	---	.9	.04	.70	.74
<u>Bromus richardsonii</u>	.03	2.6	.09	1.01	1.10
<u>Festuca arizonica</u>	.11	4.8	.73	2.50	3.23
<u>Koeleria cristata</u>	.16	13.0	2.44	3.98	6.42
<u>Muhlenbergia minutissima</u>	---	.6	---	.01	.01
<u>Muhlenbergia virescens</u>	.59	13.9	15.64	13.41	29.05
<u>Poa fendleriana</u>	1.21	40.6	29.37	28.24	57.61
<u>Poa pratensis</u>	2.05	19.1	24.31	38.43	62.74
<u>Sitanion hystrix</u>	1.27	64.4	15.85	26.46	42.31
<u>Sporobolus interruptus</u>	.06	.9	---	3.24	3.24
<u>Stipa pringlei</u>	---	.7	---	.92	.92
<u>Carex geophila</u>	.50	26.3	6.73	12.69	19.42
<u>Cyperus fendlerianus</u>	---	.2	---	.01	.01
Total Grasses and Sedges	6.03		97.06	132.58	229.64
<u>Achillea lanulosa</u>	1.01	36.3	11.14	13.91	25.05
<u>Agoseris arizonica</u>	.01	.6	.04	---	.04
<u>Antennaria aprica</u>	.03	.9	.69	1.07	1.76
<u>Artemisia ludoviciana</u>	---	.2	---	.16	.16
<u>Aster commutatus</u>	---	.2	.05	---	.05
<u>Aster foliaceus</u>	.01	.4	.49	---	.49
<u>Chaptalia alsophila</u>	.01	2.8	.11	.17	.28
<u>Cirsium wheeleri</u>	.19	15.7	2.37	6.22	8.59
<u>Erigeron divergens</u>	.01	.9	.10	.09	.19
<u>Erigeron flagellaris</u>	.05	5.7	.75	.73	1.48
<u>Erigeron formosissimus</u>	.80	23.0	9.63	21.41	31.04
<u>Gnaphalium grayi</u>	.01	.2	---	.02	.02
<u>Haplopappus croceus</u>	.01	1.1	.03	.03	.06
<u>Helenium hoopesii</u>	---	.6	---	2.69	2.69
<u>Hieracium fendleri</u>	.02	2.2	.04	.27	.31
<u>Hymenopappus mexicanus</u>	.01	.4	---	.21	.21
<u>Senecio neomexicanus</u>	.12	22.0	2.81	2.46	5.27
<u>Solidago missouriensis</u>	.01	2.2	.24	1.44	1.68
<u>Solidago sparsiflora</u>	.04	1.3	1.16	.97	2.13
<u>Taraxacum officinale</u>	.21	13.5	1.76	1.52	3.28
<u>Viguiera annua</u>	.01	2.6	.94	.60	1.54
Total Composites	2.55		32.28	53.97	86.25

Table 2. Continued.

Taxon	Cover (%)	Freq. ^a (%)	Production (kg/ha/yr)		
			Spr/ES ^b	LS/Fall ^c	NAPP ^d
<u>Astragalus tephrodes</u>	.01	.4	3.81	.02	3.83
<u>Cologania longifolia</u>	---	.2	---	.08	.08
<u>Lathyrus arizonicus</u>	.32	3.3	2.78	1.09	3.87
<u>Lotus wrightii</u>	.04	4.1	.74	2.71	3.45
<u>Lupinus argenteus</u>	.01	2.0	1.36	2.41	3.77
<u>Phaseolus parvulus</u>	---	.4	---	.05	.05
<u>Thermopsis pinetorum</u>	.01	.4	.50	---	.50
<u>Trifolium rusbyi</u>	6.98	35.9	87.48	13.99	101.47
<u>Vicia americana</u>	.38	17.2	3.51	5.33	8.84
Total Legumes	7.76		101.29	25.67	126.96
<u>Allium geyeri</u>	---	.4	---	.17	.17
<u>Apocynum androsaemifolium</u>	.01	.2	.19	---	.19
<u>Aquilegia chrysantha</u>	.03	1.1	.57	.48	1.05
<u>Arenaria confusa</u>	---	.6	.03	.01	.04
<u>Arenaria fendleri</u>	---	.2	.47	---	.47
<u>Castilleja austromontana</u>	.01	.4	---	.38	.38
<u>Ceanothus fendleri</u>	.03	.6	2.06	.77	2.83
<u>Chenopodium fremontii</u>	.01	.2	.01	---	.01
<u>Comellina dianthifolia</u>	---	.4	---	.38	.38
<u>Corallorhiza maculata</u>	---	.2	---	.28	.28
<u>Epilobium paniculatum</u>	---	2.2	.84	1.84	2.68
<u>Euphorbia chamaesula</u>	---	.2	---	.10	.10
<u>Fragaria ovalis</u>	.07	4.3	1.76	1.66	3.42
<u>Geranium caespitosum</u>	.09	11.3	.93	2.03	2.96
<u>Geranium richardsonii</u>	.06	.9	.16	1.89	2.05
<u>Geum triflorum</u>	.23	2.8	1.92	8.30	10.22
<u>Houstonia wrightii</u>	---	.2	---	.21	.21
<u>Iris missouriensis</u>	.02	.4	---	1.18	1.18
<u>Linum neomexicanum</u>	---	1.1	.02	.03	.05
<u>Myosurus aristatus</u>	---	.2	.04	---	.04
<u>Oxalis grayi</u>	---	.9	---	.02	.02
<u>Penstemon barbatus</u>	.01	.7	.73	.56	1.29
<u>Penstemon oliganthus</u>	.01	.6	.01	.19	.20
<u>Polygonum aviculare</u>	.01	1.1	.50	1.07	1.57
<u>Polygonum sawatchense</u>	.03	7.4	.88	.46	1.34
<u>Potentilla concinna</u>	.07	10.7	.50	.70	1.20
<u>Potentilla hippiana</u>	.06	2.2	1.25	2.79	4.04
<u>Prunella vulgaris</u>	.02	2.6	.56	1.08	1.64
<u>Pseudocymopterus montanus</u>	.74	32.4	1.95	9.47	11.42

Table 2. Continued.

Taxon	Cover (%)	Freq. ^a (%)	Production (kg/ha/yr)		
			Spr/ES ^b	LS/Fall ^c	NAPP ^d
<u>Rorippa curvisiliqua</u>	---	.2	.01	---	.01
<u>Rosa arizonica</u>	.65	17.6	9.49	13.76	23.25
<u>Saxifraga rhomboidea</u>	---	.2	.23	---	.23
<u>Silene scouleri</u>	.01	.9	.01	.57	.58
<u>Thalictrum fendleri</u>	.13	4.6	.89	1.07	1.96
<u>Veronica peregrina</u>	.01	.2	---	.02	.02
Total Other Herbs	2.69		26.01	51.15	77.16
<u>Pteridium aquilinum</u>	.42	3.9	18.39	30.49	48.88
Total Understory Plants	19.02		273.99	293.87	567.86

^aFrequency^bSpring/Early-summer^cLate-summer/Fall^dNet Annual Primary Production

hystrix (1.3%), Poa fendleriana (1.2%), and Achillea lanulosa (1.0%).

Frequency measures the commonness or rarity of species rather than abundance. Only 17 species occurred in 10% or more of the quadrats, and only one species (Sitanion) occurred in over 50% of the quadrats (Table 2). Fifty-five of the 81 species were found in less than 3% of the quadrats, and another 91 herbaceous species found on the study site did not occur in the frequency sample. These figures demonstrate that most understory species were very rare in this forest. The only common species--using an arbitrary criterion of 20% frequency--were Sitanion (64.4%), Poa fendleriana (40.0%), Achillea (36.3%), Trifolium (35.9%), Pseudocymopterus montanus (32.4%), Carex geophila (26.3%), Erigeron formosissimus (23.0%), and Senecio neomexicanus (22.0%).

Net annual primary production on the pine plots averaged 568 kg/ha/yr (Table 2). Grasses and sedges accounted for 40% of this total (230 kg/ha/yr); composites for 15% (86 kg/ha/yr); legumes for 22% (127 kg/ha/yr); and other herbs for 14% (77 kg/ha/yr). Among the component species, production was distributed in a log normal pattern (Figure 2). Such a pattern is typical of samples from heterogeneous, species-rich communities.

Table 3 lists some previously published estimates of total production in undisturbed Arizona ponderosa pine forests. The value found in this study (568 kg/ha/yr) appears to be higher than those listed in Table 3. However, all of the estimates of production in Table 3 are based on peak standing crops, which generally underestimate production (Kelly et al. 1974; Tumidajowicz 1973, 1976). If these peak standing

Table 3. Published estimates of total understory net annual primary production in undisturbed Arizona ponderosa pine forests.

Location, notes	NAPP ^a	Source
Wild Bill Range		
Unthinned	63	Clary, Kruse, and Larson (1975)
Unthinned	193	"
Unburned, unthinned	81	Pearson, Davis, and Schubert (1972)
Malay Gap, openings	1814	Cooper (1960b)
Beaver Creek Watershed		
Long term studies	222	Brown et al. (1974)
Unthinned	176	Clary and Ffolliott (1966)
Flagstaff vicinity		
Unburned, 1972	474	Campbell et al. (1977)
Unburned, 1974	559	"
Santa Catalina Mts.	45	Whittaker and Niering (1975)

^aNet annual primary production, in kg/ha/yr.

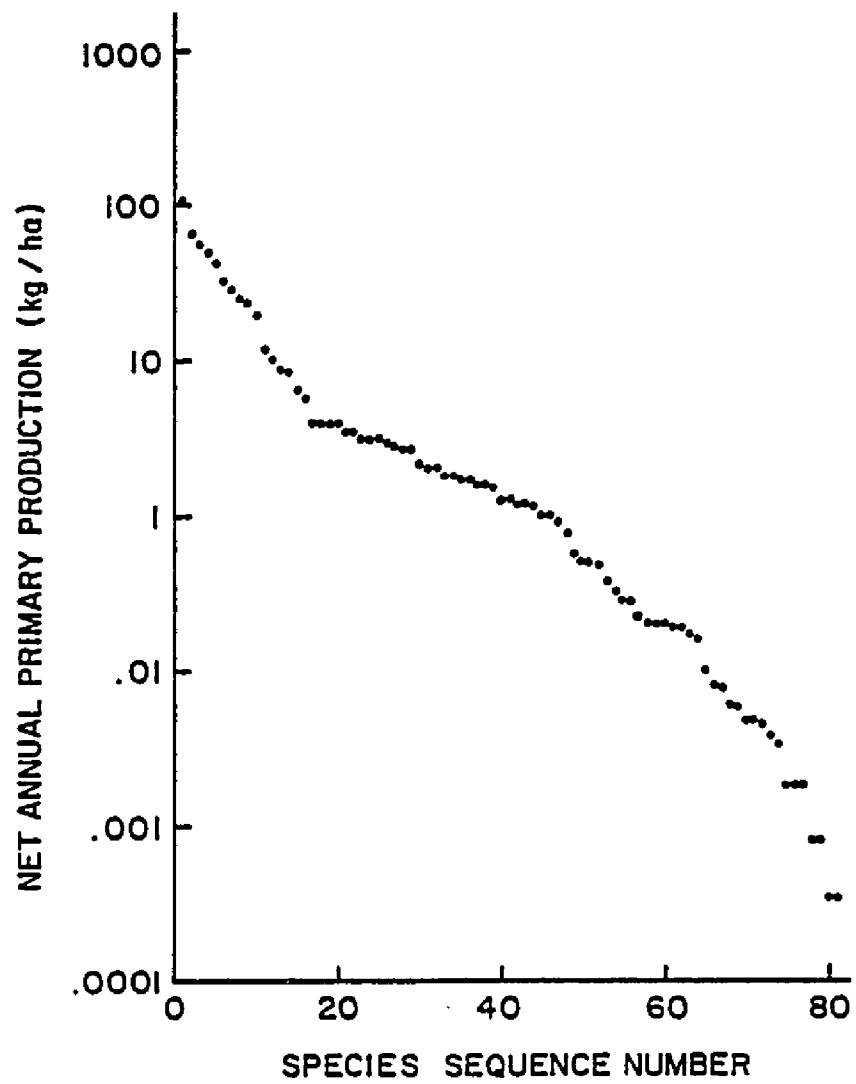


Figure 2. Dominance-diversity curve of production values for understory species on ponderosa pine plots. -- Species sequence number is a rank-ordering of species in order of decreasing net annual primary production.

crop estimates are approximately 50% too low, as suggested by the results discussed in Appendix C, then the estimate reported herein would fall within the range of published production values for undisturbed ponderosa pine understories.

The method of determining production used in this study can show seasonal trends in biomass and productivity. Those trends are illustrated in Figures 3 and 4. Despite the interest shown by forest and range scientists in understory production in ponderosa pine forests, this study is the first to demonstrate and discuss the seasonal patterns in understory production in this forest type.

Total understory biomass on the study site peaked in September (Figure 3), but was fairly high from June to October. During the growing season, plants and plant parts continuously die off as new green matter is produced. Different floristic groups showed markedly different trends. Legumes reached a maximum biomass in June and steadily declined in their standing crop for the remainder of the season. Composites and other herbs reached a maximum biomass in late summer, but grasses and sedges did not reach maximum biomass until the end of the growing season. It is clear from Figure 3 that a sample from a pine forest understory community obtained at only one time of the year cannot adequately depict the composition or production of the community.

Seasonal trends in productivity are displayed in Figure 4. Total productivity was biseasonal, but the different floristic groups each showed only one distinct peak. Legumes showed maximum production in the spring, other herbs in mid-summer, and composites and grasses and sedges in late summer. These groups demonstrated differentiation

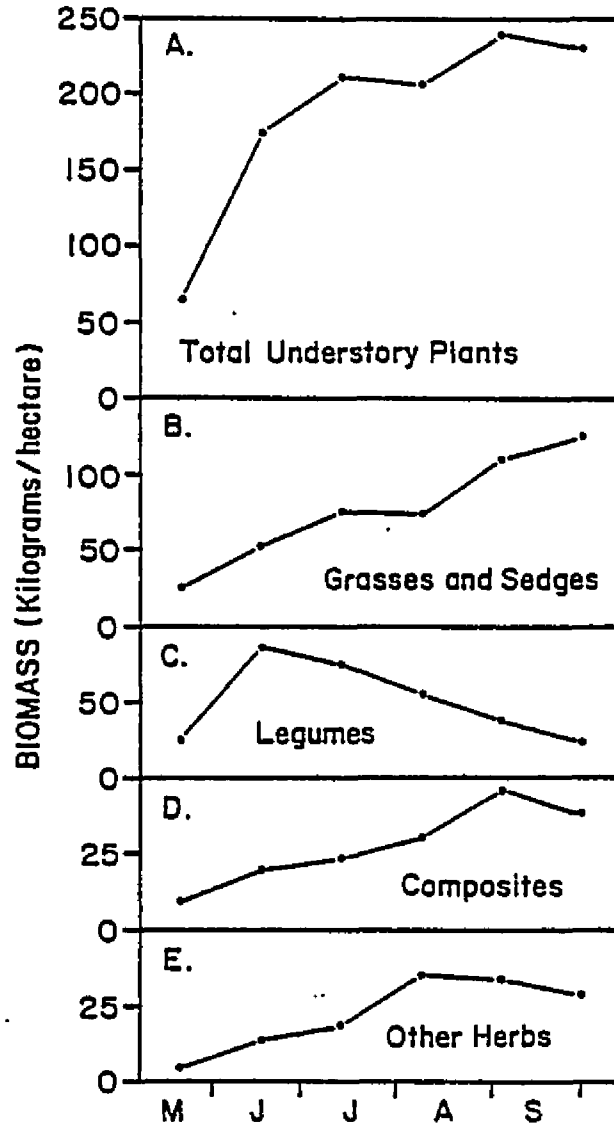


Figure 3. Seasonal trends in biomass of understory plants on ponderosa pine plots. -- Total understory plants (A), total grasses and sedges (B), total legumes (C), total composites (D), and total other herbs (E). Abscissa is the time of year, in months: May (M), June (J), July (J), August (A), and September (S).

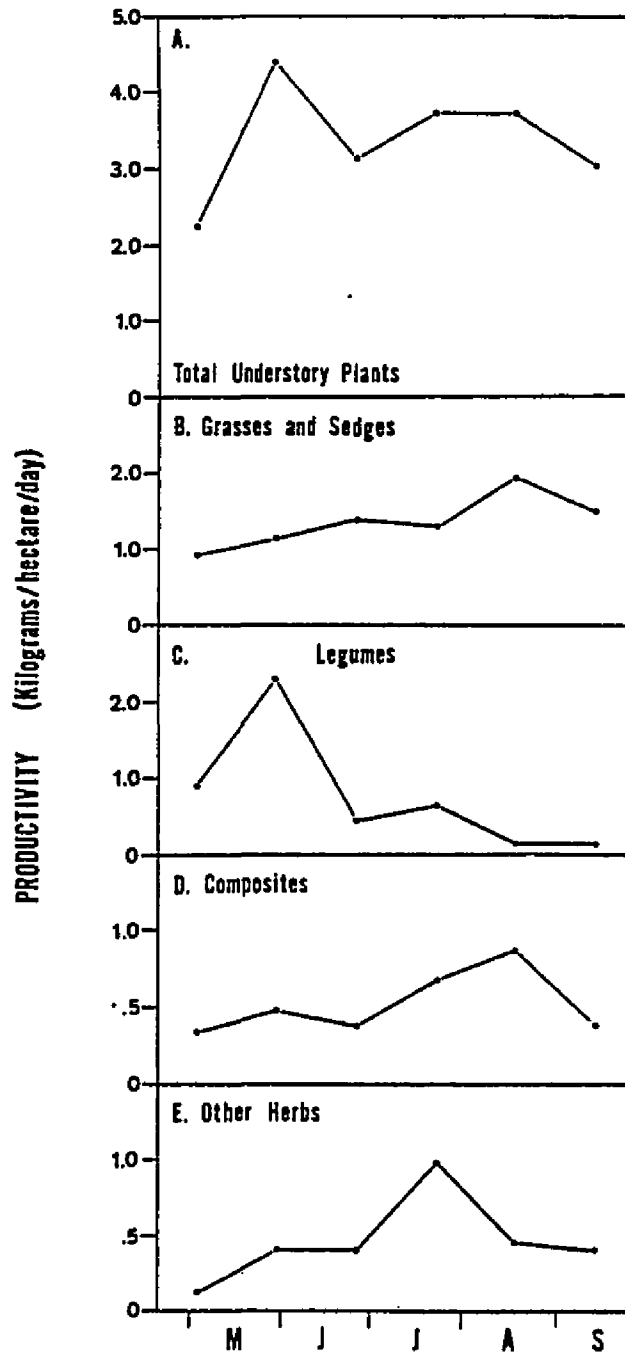


Figure 4. Seasonal trends in productivity of understory plants on ponderosa pine plots. -- Total understory plants (A), total grasses and sedges (B), total legumes (C), total composites (D), and total other herbs (E). Abscissa as in Figure 3.

in time of their maximum productivity, and hence in the time of maximum utilization of environmental resources.

Biomass and productivity values of individual species were too variable to illustrate seasonal trends. This high variability was attributable to the low frequencies of most species and to the clumped distributions of many species resulting from vegetative reproduction. Net annual primary production of individual species is divided into spring/early-summer and late-summer/fall production in Table 2.

The biseasonal pattern of total understory productivity reflects the biseasonal distribution of precipitation for the area (Figures 1, 4). A period of maximum biological activity occurs in spring when soil moisture is derived from snow melt and both soil and air temperatures are relatively low. By June, soil moisture is depleted, humidity is low and temperatures are high, and consequently productivity decreases. A second peak in biological activity occurs in mid- and late-summer, when soil moisture is recharged from convective storms. Air and soil temperatures decrease, but are still higher than those characterizing the spring season. Species appeared to respond to this seasonal heterogeneity in climate in three ways, showing high production in (1) the favorable spring season (e.g., Trifolium rusbyi); (2) the favorable late-summer season (e.g., Erigeron formosissimus, Sitanion hystrix, Pseudocymopterus montanus); and (3) both seasons (e.g., Poa fendleriana, Achillea lanulosa). It appears from the biseasonal breakdown of net annual primary production values in Table 2 that most species in this community were able to utilize both favorable seasons.

Understory/Environment Relationships

Correlation Analysis

Simple correlation coefficients between the production of total understory plants, grasses and sedges, composites, legumes, other herbs, and the fifteen most common and abundant species on the study site with overstory, litter, and soil attributes are presented in Table 4. Correlation coefficients among environmental attributes are presented in Table 5. The following discussion is based on the information contained in these two tables.

Transmissivity was strongly correlated with 13 of the 20 understory taxa. In all cases but three (Cirsium wheeleri, Vicia americana, Pteridium aquilinum) the correlations were positive, indicating that light is an important factor in the understory. Eight of the correlation coefficients between understory taxa and overhead canopy cover were significant. All these were negative, except that with Pteridium, indicating that differences in throughfall also may be important, since overhead canopy cover is a good indirect measure of throughfall (Appendix B). Six understory taxa were significantly correlated with both transmissivity and overhead canopy cover. In four of these cases, the correlations with transmissivity were higher, suggesting that light was the more important factor. Seven understory taxa were correlated with canopy height. All of the strong ($p < .01$) correlations with this overstory attribute were negative. Seven understory taxa also were correlated with basal area, six negatively. All of the seven understory taxa significantly correlated with basal area were more strongly correlated

Table 4. Simple correlation coefficients between understory production and environmental attributes.

Taxon	Trans- missivity	Overhead Canopy Cover	Canopy Height	Density	
Total Understory Plants	.629***	-.163	.017	.007	-.
Grasses and Sedges	.744***	-.491**	.299*	-.139	-.
Composites	.485**	-.403*	.101	-.082	-.
Legumes	.429**	.005	-.109	.176	.
Other Herbs	.239	-.114	-.518**	.227	-.
<u>Carex geophila</u>	.160	-.285*	-.237	.374*	-.
<u>Koeleria cristata</u>	.263*	-.045	-.202	.163	.
<u>Muhlenbergia virescens</u>	-.233	-.120	-.425**	.248	.
<u>Poa fendleriana</u>	.655***	-.597***	.207	-.008	-.
<u>Poa pratensis</u>	.663***	-.113	.091	.014	-.
<u>Sitanion hystrix</u>	-.196	-.204	.086	-.141	.
<u>Achillea lanulosa</u>	.694***	-.516**	.302*	-.092	-.
<u>Cirsium wheeleri</u>	-.389*	.175	.232	-.314*	.
<u>Erigeron formosissimus</u>	.151	-.145	-.524***	.395*	.
<u>Senecio neomexicanus</u>	.297*	-.534***	.226	-.106	-.
<u>Trifolium rusbyi</u>	.545***	-.144	-.013	.163	-.
<u>Vicia americana</u>	-.330*	.221	-.421**	.088	.
<u>Pseudocymopterus montanus</u>	.172	-.261*	.001	.028	.
<u>Rosa arizonica</u>	-.054	-.126	-.579***	.404*	-.
<u>Pteridium aquilinum</u>	-.422**	.547***	-.138	-.027	.

*significant at the 0.1 level

**significant at the .01 level

***significant at the .001 level

derstory

Density	Basal Area	01 Litter	02 Litter	Litter-fall	Surface Rock Cover	Organic Matter	Total Nitrogen	p
.007	-.251*	-.058	-.389*	.061	-.230	.526***	.484**	-.324
-.139	-.503**	-.158	-.432**	-.196	-.286*	.270*	.262*	-.454
-.082	-.234	-.170	-.234	-.148	.133	.227	.285*	-.358
.176	.018	-.067	-.196	.133	-.235	.256*	.309*	-.104
.227	-.084	-.177	-.096	-.159	-.024	.218	.189	.082
.374*	-.058	-.012	-.034	-.072	.011	-.207	-.099	-.210
.163	.049	-.029	-.195	.072	-.031	.472**	.427**	-.145
.248	.178	.042	.095	.030	-.206	.088	.069	.318
-.008	-.644***	-.465**	-.468**	-.471**	-.014	.043	.014	-.356
.014	-.302*	-.009	-.298*	.098	-.405*	.368*	.353*	-.343
-.141	.028	-.020	.265*	-.060	.111	-.320*	-.138	.207
-.092	-.504**	-.410*	-.496**	-.439**	-.082	.081	.107	-.379
-.314*	.152	.478**	.257*	.206	.094	-.263*	-.250*	.254
.395*	.057	-.305*	-.054	-.089	.281	.313*	.272*	.025
-.106	-.418*	-.238	-.250*	-.421**	.200	-.142	-.122	-.112
.163	-.073	-.230	-.350*	-.026	-.365*	.263*	.277*	-.231
.088	.146	-.031	.412*	.047	-.025	-.183	-.153	.337
.028	.028	.291*	.285*	.094	-.174	.073	.301*	-.099
.404*	-.005	-.539***	-.084	-.456**	.035	-.219	-.309*	.226
-.027	.285*	.313*	.072	.330*	-.159	.082	-.056	.251

Litter-fall	Surface Rock Cover	Organic Matter	Total Nitrogen	pH	Nitrate	Phosphate	Calcium	Magnesium
.061	-.230	.526***	.484**	-.324*	.190	.064	.271*	.132
.196	-.286*	.270*	.262*	-.454**	.141	-.086	.195	.225
.148	.133	.227	.285*	-.358*	.080	-.261*	.239	.174
.133	-.235	.256*	.309*	-.104	.135	-.138	.197	.279*
.159	-.024	.218	.189	.082	.260*	-.032	.344*	.317*
.072	.011	-.207	-.099	-.210	.175	.172	.054	-.055
.072	-.031	.472**	.427**	-.145	.101	.100	.342*	.098
.030	-.206	.088	.069	.318*	.171	.204	.348*	.277*
.471**	-.014	.043	.014	-.356*	.073	-.350*	.152	.245*
.098	-.405*	.368*	.353*	-.343*	.110	.007	.109	.229
.060	.111	-.320*	-.138	.207	-.005	-.050	.073	.108
.439**	-.082	.081	.107	-.379*	.080	-.342*	.224	.290*
.206	.094	-.263*	-.250*	.254*	-.531***	.274*	-.291*	-.359*
.089	.281	.313*	.272*	.025	.311*	-.186	.523**	.441**
.421**	.200	-.142	-.122	-.112	.021	-.163	.194	.127
.026	-.365*	.263*	.277*	-.231	.213	-.119	.239	.283*
.047	-.025	-.183	-.153	.337*	.022	-.022	-.114	-.022
.094	-.174	.073	.301*	-.099	-.159	-.019	.277*	.226
.456**	.035	-.219	-.309*	.226	.186	-.234	.233	.557***
.330*	-.159	.082	-.056	.251*	-.111	.454**	-.220	-.302*

Nitrate	Phosphate	Calcium	Magnesium	Sodium	Potassium	Sand	Clay
.190	.064	.271*	.132	.376*	-.255*	-.422**	.582***
.141	-.086	.195	.225	.311*	-.483**	-.609***	.737***
.080	-.261*	.239	.174	.064	-.418*	-.380*	.412*
.135	-.138	.197	.279*	.251*	-.465**	-.292*	.429**
.260*	-.032	.344*	.317*	.323*	-.320*	-.510**	.461**
.175	.172	.054	-.055	.075	.220	.051	-.136
.101	.100	.342*	.098	.464**	-.071	-.422**	.398*
.171	.204	.348*	.277*	.193	-.180	-.189	.073
.073	-.350*	.152	.245*	.007	-.699***	-.595***	.535***
.110	.007	.109	.229	.382*	-.322*	-.479**	.624***
-.005	-.050	.073	.108	-.203	-.282*	.201	-.181
.080	-.342*	.224	.290*	.118	-.718***	-.455**	.598***
-.531***	.274*	-.291*	-.359*	-.207	.466**	.312*	-.530***
.311*	-.186	.523**	.441**	.272*	-.360*	-.434**	.331*
.021	-.163	.194	.127	.008	-.407*	-.111	.127
.213	-.119	.239	.283*	.271*	-.607***	-.417*	.555***
.022	-.022	-.114	-.022	-.210	-.228	.007	-.202
-.159	-.019	.277*	.226	.192	-.181	-.396*	.234
.186	-.234	.233	.557***	-.016	-.357*	-.423**	.312*
-.111	.454**	-.220	-.302*	-.040	.781***	.513**	-.465**

Table 5. Simple correlation coefficients among the environmental attributes.

Attribute	Trans- missivity	Overhead Canopy Cover	Canopy Height	Density	Basal Area
Transmissivity	----				
Overhead Canopy Cover	-.512**	----			
Canopy Height	.298*	-.135	----		
Density	.005	.100	-.749***	----	
Basal Area	-.671***	.565***	-.382*	.338*	----
O1 Litter	-.158	.248*	.324*	-.306*	.238
O2 Litter	-.511**	.267*	-.030	-.121	.418*
Litterfall	-.260*	.504**	.014	.080	.553*
Surface Rock Cover	-.027	-.273*	-.100	-.022	-.187
Organic Matter	.323*	.084	-.021	.059	-.032
Total Nitrogen	.361*	-.050	.098	-.022	.036
pH	-.469**	.429**	-.390*	.127	.340*
Nitrate	.137	-.268*	-.297*	.171	-.080
Phosphate	-.145	.377*	-.066	.021	.324*
Calcium	.248*	-.193	-.282*	.374*	.007
Magnesium	.165	-.065	-.380*	.548***	.063
Sodium	.348*	-.100	-.090	.086	-.069
Potassium	-.476**	.462**	.097	-.142	.393*
Sand	-.618***	.519**	.144	-.202	.414*
Clay	.629***	-.380*	-.001	.076	-.352*

*significant at the 0.1 level

**significant at the .01 level

***significant at the .001 level

Basal Area	01 Litter	02 Litter	Litter-fall	Surface Rock Cover	Organic Matter	Total Nitrogen	pH	Nitrate
238	----							
418*	.518**	----						
553***	.692***	.367*	----					
187	-.199	-.052	-.233	----				
032	.092	-.234	.376*	.084	----			
036	.307*	.054	.448**	.056	.835***	----		
340*	.138	.314*	.073	.105	.010	-.023	----	
080	-.477**	.047	-.396*	.131	.113	.133	-.012	----
324*	.615***	.264*	.568***	-.290*	.301*	.335*	.518**	-.231
007	-.129	-.027	-.024	.213	.505**	.583***	.310*	.392*
063	-.513**	-.165	-.311*	.004	-.002	-.035	.196	.342*
069	.138	-.009	.117	-.023	.556***	.673***	.244	.293*
393*	.601***	.325*	.465**	-.097	-.108	-.067	.168	-.348*
414*	.367*	.272*	.313*	.015	-.257*	-.187	.254*	-.311*
352*	-.467**	-.350*	-.355*	-.134	.344*	.274*	-.294*	.455**

r-	Surface Rock Cover	Organic Matter	Total Nitrogen	pH	Nitrate	Phosphate	Calcium	Magnesium	Sodi
	.084	-----							
	.056	.835***	-----						
	.105	.010	-.023	-----					
	.131	.113	.133	-.012	-----				
*	-.290*	.301*	.335*	.518**	-.231	-----			
	.213	.505**	.583***	.310*	.392*	.138	-----		
	.004	-.002	-.035	.196	.342*	-.292*	.606***	-----	
	-.023	.556***	.673***	.244	.293*	.394*	.777***	.290*	-----
	-.097	-.108	-.067	.168	-.348*	.482**	-.339*	-.483**	-.069
	.015	-.257*	-.187	.254*	-.311*	.234	-.369*	-.384*	-.378*
	-.134	.344*	.274*	-.294*	.455**	-.289*	.473**	.564***	.496*

Nitrate	Phosphate	Calcium	Magnesium	Sodium	Potassium	Sand	Clay
---------	-----------	---------	-----------	--------	-----------	------	------

----	----	----	----	----	----	----	----
-.231							
.392*	.138	----	----	----	----	----	----
.342*	-.292*	.606***	----	----	----	----	----
.293*	.394*	.777***	.290*	----	----	----	----
-.348*	.482**	-.339*	-.483**	-.069	----	----	----
-.311*	.234	-.369*	-.384*	-.378*	.580***	----	----
.455**	-.289*	.473**	.564***	.496**	-.614***	-.768***	----

with either transmissivity or overhead canopy cover. There were five weakly significant correlations between understory taxa and tree density.

Among the overstory attributes there were many significant and important correlations. Basal area was significantly correlated with all other overstory attributes and therefore may be the most general measure of pine abundance on the study site. Canopy height and tree density, the two most variable stand attributes (Table 1), showed a very strong negative correlation with each other. Canopy height and tree density described an important aspect of stand structure related to stand age. Younger stands of ponderosa pine on the study site were composed of a large number of small trees while older stands contained a small number of large trees. Canopy height seemed to be the best indicator of the importance of this age-related aspect of stand structure to understory plants, since seven taxa were correlated with canopy height but only five were correlated with density, and the correlations with canopy height were generally much stronger.

Of the three measures of litter accumulation, the O1 layer was significantly correlated with seven understory taxa (four negatively), the O2 layer with 11 (seven negatively), and litterfall with five (four negatively). Thus the influence of accumulating litter on understory production was generally negative, and correlations were most often observed with the O2 layer. All three litter attributes were positively correlated with canopy height and negatively correlated with density, and the O2 layer and litterfall were both negatively correlated with transmissivity and positively correlated with basal area.

The most influential soil attributes appeared to be potassium and texture. Potassium was significantly correlated with 15 of the 20 understory taxa investigated (13 negatively), clay with 14 (12 positively), and sand with 15 (13 negatively). The numerous negative correlations between understory taxa and potassium suggest a possible inhibitory role for potassium in the understory community. However, since potassium was negatively correlated with transmissivity and positively correlated with overhead canopy cover, basal area, and all three measures of litter accumulation, the negative correlations between potassium and understory taxa could represent indirect influences of the overstory. Potassium was also negatively correlated with nitrate, calcium, magnesium, and clay and positively correlated with phosphate and sand. Clay and sand were negatively correlated with each other and both also were significantly correlated with many overstory, litter, and soil attributes. Sand was positively correlated with overhead canopy cover, basal area, O1 litter, O2 litter, litterfall and was negatively correlated with transmissivity. Clay showed the same significant correlations but with the opposite signs. These latter correlations demonstrated that ponderosa pine was more abundant on the coarser textured soils on this study site.

The remaining soil attributes were correlated with at least three of the understory taxa. Surface rock was weakly correlated with just four of the understory taxa. One important pattern that emerges from examination of the correlations among soil and overstory attributes is that the younger stands of small trees seemed to be associated with more fertile surface soils--canopy height was negatively correlated

with pH, nitrate, calcium, and magnesium. Phosphate was positively correlated with overhead canopy cover, basal area, and all three litter attributes, suggesting that phosphate levels in the surface soils may be largely derived from litterfall.

Multiple Regression Analysis

Evaluation of the relative influence of overstory, litter, and soil attributes on understory taxa by simple correlation is complicated by the numerous correlations and interactions among the environmental attributes. Multiple regression analysis, however, provides a measure of the independent contribution of each environmental attribute in accounting for the variation in production of the understory taxa. The coefficients of variation (R^2 values, expressed as percentages) of the regression analysis of the understory taxa on the environmental attributes are presented in Table 6. The last column of Table 6, headed "Multiple R^2 ", is the sum of all significant R^2 values. The regression analysis accounted for a substantial proportion of the variance in all understory taxa investigated, ranging from 32.0% for Koeleria to 80.4% for Pteridium and averaging 59.0% for all taxa. The column totals, labeled "Index of Influence", are mean R^2 values for all environmental attributes. This index is intended only as an indication of an environmental attribute's comparative influence in the understory community. For all multiple regression coefficients with a significant R^2 , the sign of the regression coefficient was the same as the simple correlation coefficient (Table 4), except where otherwise noted.

Table 6. Multiple regression coefficients of determination (R^2) of understory production on environmental attributes.

Taxon	Trans- missivity	Overhead Canopy Cover	Canopy Height	Density
Total Understory Plants	39.4***	1.2	2.4	5.9*
Grasses and Sedges	55.3***	3.5*	0.3	2.4
Composites	23.5**	---	9.8*	5.1
Legumes	6.6*	3.3	2.1	2.7
Other Herbs	7.9*	2.1	26.8**	8.9*
<u>Carex geophila</u>	6.1*	10.5*	2.1	14.0*
<u>Koeleria cristata</u>	0.3	1.4	2.9	2.1
<u>Muhlenbergia virescens</u>	2.9	6.5*	18.0*	5.8
<u>Poa fendleriana</u>	2.5	2.7	1.1	0.6
<u>Poa pratensis</u>	43.9***	0.1	2.3	2.6
<u>Sitanion hystrix</u>	0.2	6.1	2.2	2.6
<u>Achillea lanulosa</u>	16.0***	0.7	5.5*	1.3
<u>Cirsium wheeleri</u>	4.4	0.2	1.1	5.2
<u>Erigeron formosissimus</u>	2.1	4.1	27.5**	4.6
<u>Senecio neomexicanus</u>	1.0	28.5**	3.4	0.8
<u>Trifolium rusbyi</u>	6.8*	0.3	0.4	0.1
<u>Vicia americana</u>	0.6	2.2	17.8*	1.3
<u>Pseudocymopterus montanus</u>	2.5	3.1	2.4	1.3
<u>Rosa arizonica</u>	3.9*	0.4	33.5***	1.1
<u>Pteridium aquilinum</u>	---	3.9*	4.6*	2.5*
Index of Influence (mean R^2)	11.3	4.0	8.3	3.5

*significant at the 0.1 level
 **significant at the .01 level
 ***significant at the .001 level

f determination (R^2)

Canopy Height	Density	Basal Area	O1 Litter	O2 Litter	Litter-fall	Surface Rock Cover	Organic Matter	Total Nitrog
2.4	5.9*	2.2	---	0.6	0.4	6.1*	11.7**	---
0.3	2.4	0.6	0.1	1.8	1.3	4.7*	0.2	0.1
9.8*	5.1	10.6*	0.9	0.4	---	0.7	1.3	3.2
2.1	2.7	7.5*	0.2	0.2	15.6*	6.2*	0.2	2.1
26.8**	8.9*	---	4.4*	1.3	0.8	---	1.2	1.6
2.1	14.0*	2.8	1.8	1.4	---	0.9	3.4	4.1
2.9	2.1	4.6	2.0	0.2	2.4	0.2	22.3**	0.1
18.0*	5.8	3.0	4.0	3.5	1.5	6.2	2.2	2.7
1.1	0.6	16.1**	2.7	1.1	0.4	2.5	0.7	0.1
2.3	2.6	0.5	0.4	0.1	7.1*	15.0**	1.1	---
2.2	2.6	0.4	4.2	8.3*	1.6	0.2	10.2*	0.1
5.5*	1.3	1.3	0.9	2.1	---	1.3	0.9	1.2
1.1	5.2	0.5	1.4	0.6	0.3	0.9	---	1.7
27.5**	4.6	2.5	2.1	2.8	0.6	0.5	0.5	0.8
3.4	0.8	1.7	1.2	2.2	0.1	1.1	1.5	3.5
0.4	0.1	2.7	0.1	3.7	2.1	18.1**	0.2	6.7*
17.8*	1.3	1.9	0.1	15.9*	0.4	0.8	---	---
2.4	1.3	0.5	21.9**	2.0	4.6*	3.6	---	3.3
33.5***	1.1	0.1	0.9	1.0	20.1**	0.9	0.3	0.4
4.6*	2.5*	1.6	---	4.3*	0.4	1.0	1.5	---
8.3	3.5	3.1	2.5	2.7	3.0	3.5	3.0	1.6

er-	Surface Rock Cover	Organic Matter	Total Nitrogen	pH	Nitrate	Phosphate	Calcium	Magnesium	Sodi
	6.1*	11.7**	---	2.6	0.3	1.1	1.0	1.3	1.1
	4.7*	0.2	0.1	0.7	0.2	0.6	0.1	0.7	2.3
	0.7	1.3	3.2	2.6	3.4	0.6	5.2	0.3	2.3
	6.2*	0.2	2.1	4.4	0.2	2.6	0.2	5.7*	2.4
	---	1.2	1.6	1.9	0.2	0.5	1.8	0.1	1.6
	0.9	3.4	4.1	4.9*	3.3	4.2	2.3	0.7	2.2
	0.2	22.3**	0.1	2.8	3.2	0.6	1.1	0.1	3.3
	6.2	2.2	2.7	1.7	2.7	2.0	8.5*	1.2	6.8
	2.5	0.7	0.1	0.1	2.5	0.9	1.2	0.2	0.3
	15.0**	1.1	---	1.6	0.4	---	2.7	6.1*	1.7
	0.2	10.2*	0.1	4.5	0.1	4.6	1.4	0.5	0.5
	1.3	0.9	1.2	0.2	0.6	---	1.9	1.3	1.0
	0.9	---	1.7	0.1	28.2**	1.0	0.3	2.0	---
	0.5	0.5	0.8	8.5*	1.3	---	15.3*	4.4	3.1
	1.1	1.5	3.5	0.8	1.2	2.7	7.6*	0.7	1.2
	18.1**	0.2	6.7*	2.2	1.1	1.4	0.1	1.7	2.1
	0.8	---	---	5.4*	2.2	0.3	13.0*	2.8	---
	3.6	---	3.3	3.0	3.9	6.6*	0.7	9.9*	4.2
*	0.9	0.3	0.4	0.4	4.9*	0.5	0.9	5.2*	0.8
	1.0	1.5	---	2.0	4.1*	0.3	2.1	0.5	0.7
	3.5	3.0	1.6	2.5	3.2	1.5	3.4	2.3	1.9

ate	Phosphate	Calcium	Magnesium	Sodium	Potassium	Sand	Clay	Multiple R ²
	1.1	1.0	1.3	1.1	2.4	2.5	---	63.1
	0.6	0.1	0.7	2.3	0.5	0.1	12.0**	75.5
	0.6	5.2	0.3	2.3	4.5	0.3	1.1	44.0
	2.6	0.2	5.7*	2.4	21.6**	2.7	1.8	55.7
	0.5	1.8	0.1	1.6	---	1.5	21.2**	69.3
	4.2	2.3	0.7	2.2	24.4**	3.3	2.5	59.8
	0.6	1.1	0.1	3.3	2.4	9.9*	1.2	32.0
	2.0	8.5*	1.2	6.8*	2.4	4.0	---	39.8
	0.9	1.2	0.2	0.3	48.9***	0.6	0.1	65.0
	---	2.7	6.1*	1.7	0.8	0.4	4.5*	76.5
	4.6	1.4	0.5	0.5	10.1*	14.0*	0.7	42.7
	---	1.9	1.3	1.0	51.6***	0.5	0.1	73.1
**	1.0	0.3	2.0	---	3.6	3.5	10.5*	38.7
	---	15.3*	4.4	3.1	0.2	1.5	4.7*	55.9
	2.7	7.6*	0.7	1.2	9.0*	3.8	1.5	45.1
	1.4	0.1	1.7	2.1	36.8***	1.4	0.1	68.4
	0.3	13.0*	2.8	---	11.5*	0.9	1.7	63.5
	6.6*	0.7	9.9*	4.2*	0.2	15.6*	2.0	62.8
*	0.5	0.9	5.2*	0.8	2.1	3.5	---	67.7
*	0.3	2.1	0.5	0.7	61.0***	1.1	0.7	80.4
	1.5	3.4	2.3	1.9	14.7	3.6	3.3	

Soil exchangeable potassium had the highest general influence, accounting for the largest proportion of the variance in total legumes, Carex geophila, Poa fendleriana, Achillea lanulosa, Trifolium rusbyi, and Pteridium aquilinum. The sign of the corresponding correlation coefficient was positive for Pteridium and Carex and negative for the other taxa. Potassium also accounted for a significant proportion of the variance in Sitanion hystrix, Senecio neomexicanus, and Vicia americana; the corresponding correlation coefficients were negative. Since similar results were obtained with less extensive sampling from the previous growing season (S. P. McLaughlin, unpubl. data), the analysis of field data suggests the hypothesis that high exchangeable potassium was inhibitory to many understory taxa. The mechanism of such interference could be associated with phosphate uptake. Lettuce bioassays have shown that phosphorus is the most limiting nutrient in soils derived from the same parent materials in nearby unburned ponderosa pine forests (Wagle and Kitchen 1972) and high exchangeable potassium may interfere with the uptake of phosphorus and magnesium (Ravina and Markus 1975).

The distribution of potassium in the soil is probably controlled by ponderosa pine trees. The amount of potassium in the upper soil layer was highest in stands high in overhead canopy cover, basal area, and litterfall (Table 4). Potassium is known to be readily leached from forest canopies (Ovington 1958; Madgwick and Ovington 1959; Attiwell 1966; Abee and Lavender 1972; Eaton, Likens, and Bormann 1973), and D. M. Hendricks (Prof. of Soil Science, University of Arizona, personal communication) has shown that potassium decreases with soil depth in similar soils on the Beaver Creek Watershed in Arizona. Such

observations suggest that pines absorb potassium throughout the soil profile and redistribute it to the upper horizons by subsequent canopy leaching and litterfall. Thus the effects of potassium in the soil on understory plants ultimately can be attributed to the pine stand.

Transmissivity had the next highest general influence on understory production, accounting for the largest proportion of the variance in total understory plants, grasses and sedges, composites, and Poa pratensis. These relationships were all positive. Transmissivity was also important for total legumes, other herbs, Carex, Trifolium, and Rosa arizonica. The only negative relationship was with Rosa. Light penetration below the canopy was thus an important factor to these taxa.

Canopy height accounted for the largest proportion of the variance in total other herbs, Muhlenbergia virescens, Erigeron formosissimus, Vicia, and Rosa. All of these relationships were negative, indicating a preference in these taxa for dense stands of small trees. Total composites, Achillea, and Pteridium also were significantly related to this stand attribute, with Pteridium showing a negative relationship. The ecological significance of canopy height may be attributable to the more favorable nutrient status of surface soils in the younger stands. Another likely possibility is that species negatively correlated with canopy height may be sensitive to the effects of cattle grazing, a factor not directly investigated in this study. Cattle are known to prefer to graze in older, more accessible, park-like open stands of tall trees (Arnold 1950; Reynolds 1969).

All other environmental attributes had a lower general influence on understory plants. Organic matter was the most important

attribute for Koeleria cristata; sand for Sitanion; soil nitrate for Cirsium; overhead canopy cover for Senecio; and the O1 litter layer for Pseudocymopterus montanus.

In general, litter did not appear to have the significant negative influence on understory plants it is generally believed to have. The relationship with O1 litter and Pseudocymopterus was positive, and the only other significant regression involving O1 litter (with total other herbs) was also positive. For Sitanion, Vicia, and Pteridium, the O2 layer was significant, but the relationship was negative only for Pteridium. Litterfall was a significant attribute for total legumes, Poa pratensis, Pseudocymopterus, and Rosa, and the regression coefficients were negative for only Pseudocymopterus and Rosa. Litter attributes were strongly correlated with many overstory and soil attributes, and, after adjusting for the variance accounted for by these attributes, the influence of litter accumulation was more often beneficial than detrimental to many understory taxa.

The influence of soil texture and exchangeable cations other than potassium also was generally of less importance after adjusting for the effects of other attributes. Clay was significant for total grasses and sedges, other herbs, Poa pratensis, Cirsium, and Erigeron, and sand was significant for Koeleria, Sitanion, and Pseudocymopterus. Of these taxa, grasses and sedges, Koeleria, Poa pratensis, Erigeron, and Pseudocymopterus were positively related to finer textured soils. Organic matter was significant for total understory plants, Koeleria, and Sitanion, and total nitrogen was significant for Trifolium. Calcium, magnesium, and sodium were of minor significance for eight of the

understory taxa, and most of these relationships were positive. Thus, greater production for many taxa was found on the finer textured soils with their associated higher cation exchange capacity and greater water retention.

Basal area was a significant attribute only for total composites, legumes, and Poa fendleriana. The relationship with legumes was positive. Basal area is the stand attribute most often used to predict stand biomass. If basal area is the best estimator of root biomass, which seems reasonable, then basal area should be a good indirect measure of competition for soil water and nutrients. If this hypothesis is correct, the results of the regression analysis suggest that such competition is not an important factor in this community. Berndt and Gibbons (1958) found that Muhlenbergia montana and Festuca arizonica were rooted at shallower depths than ponderosa pine in deep soils in Colorado. Such partitioning of the rooting zone would be the principal mechanism of avoiding competition between ponderosa pine and understory plants. In areas of shallower soils, belowground competition should be more intense and basal area should then be a more important stand attribute in determining understory production.

Surface rock cover was important to total understory plants, grasses and sedges, legumes, Poa pratensis, and Trifolium; these relationships were all negative. Surface rock was probably a good indicator of rock in the soil profile, and these taxa probably preferred non-stony soils.

Nitrate, phosphate, and pH did not appear to have much direct influence on understory production. The large R^2 value of nitrate for

Cirsium was for a negative relationship; the smaller significant R^2 values were negative for Rosa and positive for Pteridium. The one significant R^2 value of phosphate with Pseudocymopterus was positive. Significant relationships with pH were positive for Vicia and negative for Carex and Erigeron. Since these variables are all related to soil nutrient status, it seems reasonable to conclude that nutrient status is generally not a limiting factor to understory plants in this forest community.

Atypical Species

The general patterns on the study site were that most understory species had higher production in either stands with high light penetration and low soil potassium or in younger stands. Three of the species investigated, Carex geophila, Cirsium wheeleri, and Pteridium aquilinum, did not follow these general patterns.

Carex geophila was somewhat unique in being positively related to soil potassium. This species may have a tolerance for high soil potassium and therefore was able to exploit environments relatively unavailable to other competing species. Although soil potassium and transmissivity were negatively correlated with each other, the production of Carex was positively related to transmissivity after adjusting for the variance accounted for by soil potassium.

The negative correlations of Cirsium wheeleri with nitrate and clay, as well as with soil organic matter, total nitrogen, calcium, and magnesium, suggest this species is adapted to nutrient poor soils. Many members of the genus Cirsium are pioneer species typically occurring on

nutrient poor soils. It is interesting that Cirsium wheeleri also occurred on such soils in this community despite the fact such soils were strongly correlated with high canopy cover, low transmissivity, and high basal area. Cirsium's apparent tolerance for poorer soils and low light allowed it to grow where other understory species were less abundant, thus avoiding competition.

Pteridium aquilinum had a relatively high production (48.9 kg/ha/yr) but was not particularly common, occurring in only 4.6% of the quadrats. Pteridium, like Carex, was positively related to soil potassium, and this was the most significant attribute associated with its production. Associated with this positive relationship with potassium, Pteridium showed a positive correlation with overhead canopy cover, basal area, O1 litter, and litterfall, and a negative relationship with transmissivity. Pteridium is usually considered a seral species, often dominating burned and cleared land where light intensities are high and competition with trees is minimal (Gliessman 1976). Pteridium had relatively high cover on only four of the 30 pine plots. Since these plots all had a very low cover of other understory plants, it is possible that competition with other herbaceous plants limits Pteridium elsewhere. Gliessman (1976) found that Pteridium maintains its dominance in open spaces by allelopathic suppression of competing herbaceous species. Perhaps at low densities this mechanism is ineffective, and because Pteridium appeared to tolerate high soil potassium, it occurred in this community in stands with high canopy cover and high basal area.

CONCLUSIONS

The most important overstory influences on understory plants were associated with light reduction below the canopy, soil potassium, and stand age. Exchangeable soil potassium was strongly correlated with many species, typically negatively. Soil potassium was also strongly correlated with many overstory attributes, and it seems reasonable to hypothesize that leaching of the canopy determines the distribution of potassium in the upper soil horizon. The mechanism of high potassium inhibition may be interference with the uptake of inorganic phosphorus and magnesium. Many species were more abundant in the younger, dense stands of small trees, possibly due to the higher nutrient status of the surface soils of such stands, or to cattle grazing patterns.

Many attributes of the understory environment that showed strong simple correlations with understory production may not have a direct influence on most understory plants. This was often the case for soil texture and litter in this community. Clay content was positively correlated with the majority of understory taxa examined, but was negatively correlated with more influential overstory attributes and soil potassium. Similarly, litter attributes were negatively correlated with many understory taxa but positively correlated with overstory attributes and soil potassium. After adjusting for the variance accounted for by the more influential attributes, the partial correlations of production with clay and litter were not significant for most understory taxa.

Data presented in this study do not support the notion that light is a universally important factor in the understory community. Although some attributes of the environment did have a more general influence on understory production, there was no evidence that a single factor, such as light, controlled the distribution of the majority of understory plant species. Such a situation would result in intense competition. The data do show a complex pattern of niche-differentiation among the 15 most common and abundant species with respect to overstory, litter, and soil attributes. That is, no two species showed the same combination of significant environmental attributes (Table 6). The bi-seasonal distribution of precipitation provided additional opportunities for niche-differentiation along a temporal or seasonal gradient (Table 2, Figures 3, 4).

The basis of the concept of niche-differentiation is the specialization of species along habitat, resource, and temporal gradients to reduce competition (Whittaker 1975). The heterogeneity in stand structure of ponderosa pine forests, combined with the temporal heterogeneity in precipitation during the growing season, provide many opportunities for niche-differentiation in the understory community, resulting in the very high diversity of understory species found in that community.

APPENDIX A

LIST OF THE VASCULAR FLORA OF THE STUDY SITE¹

Apocynaceae

Apocynum androsaemifolium L.

Boraginaceae

Hackelia floribunda (Lehm.) Johnst.

Lithospermum multiflorum Torr.

Campanulaceae

Campanula rotundifolia L.

Caryophyllaceae

Arenaria confusa Rydb.

A. fendleri Gray

Cerastium nutans Raf.

Drymaria depressa Greene

Silene scouleri Hook.

Chenopodiaceae

Chenopodium fremontii Wats.

C. incisum Poir

C. rubrum L.

Commelinaceae

Commelina dianthifolia Delile

Tradescantia pinetorum Greene

Compositae

Achillea lanulosa Nutt.

Agoseris arizonica Greene

A. glauca (Pursh) D. Dietr.

Antennaria aprica Greene

Artemisia ludoviciana Nutt.

Aster commutatus (Torr. & Gray) Gray

A. foliaceus Lindl.

Bahia dissecta (Gray) Britton

Brickellia grandiflora (Hook.) Nutt.

Chaptalia alsophila Greene

Cirsium drummondii Torr. & Gray

1. Nomenclature follows Kearney and Peebles (1960).

Compositae--continued

Cirsium wheeleri (Gray) Petrak
Crepis glauca (Nutt.) Torr. & Gray
Erigeron canadensis L.
E. divergens Torr. & Gray
E. flagellaris Gray
E. formosissimus Greene
E. oreophilus Greenm.
E. platyphyllus Greene
Gnaphalium grayi Nels. & Macbr.
G. macounii Greene
Haplopappus croceus Gray
H. gracilis (Nutt.) Gray
Helenium hoopesii Gray
Hieracium fendleri Schultz Bip.
Hymenopappus mexicanus Gray
Lactuca serriola L.
Senecio actinella Greene
S. bigelovii Gray
S. neomexicanus Gray
S. wootonii Greene
Solidago missouriensis Nutt.
S. sparsiflora Gray
Taraxacum officinale Weber
Townsendia formosa Greene
Tragopogon pratensis L.
Viguiera annua (Jones) Blake
V. multiflora (Nutt.) Blake
Wyethia arizonica Gray
Xanthocephalum wrightii Gray

Convolvulaceae

Convolvulus arvensis L.

Cruciferae

Rorippa curvisiliqua (Hook.) Bessey
Thelypodium longifolium (Benth.) Wats.
Thlaspi fendleri Gray

Cyperaceae

Carex athrostachya Olney
C. geophila Mackenz.
C. lanuginosa Michx.
C. petasata Dewey
C. rusbyi Mackenz.
C. siccata Dewey

Ericaceae

Chimaphila umbellata (L.) Nutt.
Monotropa latisquama (Rydb.) Hulten

Ericaceae--continued

Pterospora andromedea Nutt.
Pyrola virens Schweigg.

Euphorbiaceae

Euphorbia chamaesula Boiss.
E. serpyllifolia Pers.

Fagaceae

Quercus gambelii Nutt.

Gentianaceae

Gentiana strictiflora (Rydb.) A. Nels.
Halenia recurva (J. E. Smith) Allen

Geraniaceae

Geranium caespitosum James.
G. richardsonii Fisch. & Trautv.

Gramineae

Agropyron subsecundum (Link) Hitchc.
Agrostis scabra Willd.
Blepharoneuron tricholepis (Torr.) Nash
Bromus inermis Leyss.
B. porteri (Coul.) Nash
B. richardsonii Link
Calamagrostis canadensis (Michx.) Beauv.
Danthonia intermedia Vasey
Deschampsia caespitosa (L.) Beauv.
Festuca arizonica Vasey
F. ovina L.
Hierochloe odorata (L.) Beauv.
Hordeum brachyantherum Nevski
H. jubatum L.
Koeleria cristata (L.) Pers.
Muhlenbergia minutissima (Steud.) Swallen
M. montana (Nutt.) Hitchc.
M. virescens (H.B.K.) Kunth
M. wrightii Vasey
Panicum bulbosum H.B.K.
Phleum pratense L.
Poa compressa L.
P. fendleriana (Steud.) Vasey
P. pratensis L.
Sitanion hystrix (Nutt.) J. G. Smith
Sporobolus interruptus Vasey
Stipa pringlei Scribn.

Iridaceae

Iris missouriensis Nutt.
Sisyrinchium demissum Greene

Juncaceae

Juncus balticus Willd.
J. interior Weig.

Labiatae

Mentha arvensis L.
Monarda menthaefolia Graham
Prunella vulgaris L.

Leguminosae

Astragalus humistratus Gray
A. tephrodes Gray
Cologania longifolia Gray
Dalea filiformis Gray
Lathyrus arizonicus Britton
L. graminifolius (Wats.) White
Lotus wrightii (Gray) Greene
Lupinus argenteus Pursh
L. kingii Wats.
Melilotus officinalis (L.) Lam.
Phaseolus parvulus Greene
Robinia neomexicana Gray
Thermopsis pinetorum Greene
Trifolium rusbyi Greene
Vicia americana Muhl.

Liliaceae

Allium geyeri Wats.
Anthericum torreyi Baker
Calochortus gunnisonii Wats.

Linaceae

Linum lewisii Pursh
L. neomexicanum Greene

Loranthaceae

Arceuthobium vaginatum (H.B.K.) Eichler

Malvaceae

Sidalcea neomexicana Gray

Nyctaginaceae

Oxybaphus comatus (Small) Weatherby

Onagraceae

Epilobium adenocaulon Hausskn.
E. paniculatum Nutt.
Gaura coccinea Nutt.
Oenothera caespitosa Nutt.
O. hookeri Torr. & Gray
O. laciniata Hill

Orchidaceae

Corallorhiza maculata Raf.

Oxalidaceae

Oxalis grayi (Rose) Knuth

Pinaceae

Pinus ponderosa Lawson
P. strobiformis Engelm.
Pseudotsuga menziesii (Mirbel) Franco.

Polemoniaceae

Ipomopsis aggregata (Pursh) V. Grant

Polygonaceae

Polygonum aviculare L.
P. bistortoides Pursh
P. douglasii Greene
P. sawatchense Small
Rumex altissimus Wood

Polypodiaceae

Pteridium aquilinum (L.) Kuhn

Ranunculaceae

Aquilegia chrysantha Gray
Myosurus aristatus Benth.
Ranunculus cardiophyllus Hook.
Thalictrum fendleri Engelm.

Rhamnaceae

Ceanothus fendleri Gray

Rosaceae

Fragaria ovalis (Lehm.) Rydb.
Geum triflorum Pursh
Potentilla concinna Richards.
P. hippiana Lehm.
P. pulcherrima Lehm.
Rosa arizonica Rydb.

Rubiaceae

Houstonia wrightii Gray

Salicaceae

Populus tremuloides Michx.

Saxifragaceae

Saxifraga rhomboidea Greene

Scrophulariaceae

Castilleja austromontana Standl. & BlummerOrthocarpus luteus Nutt.Pedicularis centranthera GrayP. parryi GrayPenstemon barbatus (Cav.) RothP. oliganthus Woot. & Standl.P. virgatus GrayVerbascum thapsus L.Veronica peregrina L.

Valerianaceae

Valeriana edulis Nutt.

Verbenaceae

Verbena macdougalii Heller

Umbelliferae

Perideridia parishii (Coul. & Rose) Nels. & Macbr.Pseudcymopterus montanus (Gray) Coul. & Rose

APPENDIX B

OVERSTORY ATTRIBUTES, LIGHT, THROUGHFALL, AND THE INTERPRETATION OF OVERSTORY/UNDERSTORY RELATIONSHIPS

The cover and production of forest understory plants have been related to various overstory attributes. In southwestern ponderosa pine forests decreases in understory production have been related to increases in pine canopy cover (Arnold 1950), basal area (Reynolds 1969), and production (Ffolliott and Clary 1974). The relationships indirectly reflect factors which are significant in the understory environment--light penetration, throughfall precipitation, or competition for soil water and nutrients.

More precise interpretations of overstory/understory relationships would be possible if direct measurements of light and throughfall were available. However, it is impractical to simultaneously measure understory production, light, and throughfall on the large number of plots required to accurately estimate production. An alternative approach is to determine what overstory attributes are the best indirect measures of light penetration and throughfall.

In previous studies conducted in ponderosa pine forests, Johnson (1942) found a significant variation in throughfall between watersheds which he attributed to variation in the density of the crown canopy. Rowe and Hendrix (1951) suggested that variation in

throughfall within a stand depended both on crown drip and on canopy characteristics of the surrounding stand, rather than on cover immediately above the gauge. In the data of Alden and Curtis (1957), there was a significant ($p < .005$) relationship between percentage throughfall and basal area on nine ponderosa pine watersheds in Arizona. After adjusting for gross rainfall, Orr (1972) found a relationship between throughfall and canopy cover measured with a hemispherical (ultra-wide angle) camera. For conifer stands in general, attempts to correlate interception of rainfall with basal area "have not been very successful" (Helvey 1974).

Solomon, Ffolliott, and Thompson (1976) reported a curvilinear relationship between transmission (percentage of incident radiation penetrating the canopy to the forest floor) and basal area. However, within the range of basal areas they actually examined, a simple linear regression provided a better fit. Although the authors recommended basal area as a predictor of transmissivity (permeability of the canopy to light), they did not investigate any direct measurements of canopy cover. Muller (1971) also found a significant relationship between transmission and basal area in a ponderosa pine plantation in California. But he measured basal area in a rotating plot or "zone of influence" of variable size and position, depending on canopy height, solar azimuth and altitude, and time of day.

Since no study to date has compared various overstory attributes with both light penetration and throughfall in southwestern ponderosa pine forests, the objective of this study was to determine and

compare the relationships of basal area and three measurements of canopy cover to light and throughfall in an Arizona ponderosa pine forest, and to discuss how the results can be applied to the interpretation of overstory/understory relationships.

Methods

Twenty-one rectangular plots (.56 by 1.06 m) were established in a broad range of pine canopy and stand conditions. On each plot, four cylindrical cans (13.5 cm height by 10 cm diameter) for collecting throughfall and canopy drip were randomly positioned. Plots were enclosed in portable exclusion cages to prevent disturbance by animals.

Basal area was measured from the center of each plot with a 1:25 angle-gauge (Grosenbaugh 1952), 75 cm long with a 3 cm crosspiece. Two measurements of canopy cover were determined with a spherical densiometer (Lemmon 1956). One measurement was the average of readings of canopy cover taken at all four corners of the plot. The other measurement was the average of readings of open sky taken at the center of the plot facing in the east, south, and west directions. The former measurement is referred to herein as 360° canopy cover; the latter as ESW canopy open. A third measurement of canopy cover was obtained from photographs of the canopy directly over the plot taken with a 35 mm camera with a 50 mm lens. The long dimension of the film frame corresponded with the long dimension of the plot. Overhead canopy cover was estimated from the photographs using a rectangular grid overlay.

The 50 mm lens has a taking angle of 46° . The photographs therefore depict all canopy overlap within $\pm 23^{\circ}$ of the vertical.

The taking angle of the spherical densiometer is approximately 123° , or $\pm 61.5^{\circ}$ from the vertical. Thus, the photographs provided a measurement of the canopy cover directly overhead, while the spherical densiometer provided a broader, more wide-angle measurement of canopy cover.

Light intensity on each plot was measured on 18-19 May, 1977, using a cadmium-selenium cell light meter with a spherical diffuser. Both days were cloudless. Readings were taken every half-hour on each plot and summed to give a daily total. These totals were expressed as percentages of full sunlight, as measured in the center of a large, open meadow on the study site.

Throughfall data were collected from 15 May to 1 October, 1977. Cans were emptied approximately once every two weeks after the onset of summer rains in July. Seven ml of oil were added at the beginning and after each measurement to retard evaporation.

Results and Discussion

The ranges of overstory attributes for the 21 plots were: basal area, 0 to $68 \text{ m}^2/\text{ha}$; 360° canopy cover, 0.7 to 82.4%; ESW canopy open, 16.2 to 96.4%; and overhead canopy cover, 0 to 63.2%. Light penetration varied from 32.5 to 95.3% of full sunlight; throughfall varied from 211 to 379 mm over the 140 day period of collection.

All four overstory attributes were significantly related to throughfall and light penetration (Table 7). A χ^2 test (Zar 1974) showed that the absolute values of the simple correlation coefficients were not significantly different at the .05 level, probably because all four overstory attributes were significantly correlated with each other

Table 7. Relationships of throughfall and light penetration to basal area and canopy cover. -- Coefficients of determination for simple and stepwise multiple regression.

Overstory attribute	Throughfall		Light	
	Simple R ²	Multiple R ²	Simple R ²	Multiple R ²
Basal area	.399*	.001	.443**	.009
Overhead Canopy Cover	.661**	.661**	.555**	.007
360° Canopy Cover	.562**	.005	.650**	.004
ESW Canopy Open	.480**	.001	.736**	.736**

*significant at the .01 level

**significant at the .001 level

Table 8. Simple correlation coefficients among overstory attributes.

Overstory attribute	Basal Area	Overhead Canopy Cover	360° Canopy Cover	ESW Canopy Open
Basal Area	----			
Overhead Canopy Cover	.718	----		
360° Canopy Cover	.782	.882	----	
ESW Canopy Open	-.698	-.822	-.943	----

(Table 8). Multiple regression analysis (Table 7) showed that after accounting for the variation in throughfall explained by overhead canopy cover and for the variation in light explained by ESW canopy open, no other variables explained a significant proportion of the variance in either throughfall or light. Apparently, only the canopy directly over a plot is effected in preventing precipitation from reaching that plot. This result is not in agreement with the conclusions of Rowe and Hendrix (1951). Although Solomon et al. (1976) suggest basal area as a good predictor of transmissivity, the results of this study suggest that ESW canopy open is the best indicator of light penetration.

The results of this study can be usefully applied to the interpretation of overstory/understory relationships. A best fit of understory cover or production with ESW canopy open would indicate that light was the limiting ecological factor. A best fit of understory abundance with overhead canopy cover would indicate that moisture was the limiting factor. Basal area is the overstory attribute most often used to predict tree and stand biomass. If basal area is also the best indirect indicator of root biomass, then it should be strongly related to competition for soil water and nutrients. If this is the case, a best fit of understory abundance with basal area would indicate that competition with the overstory was the limiting factor. There is no a priori reason to suspect that all understory species or ecological groups would respond similarly to these three overstory attributes, and thus be limited by the same factors.

APPENDIX C

DETERMINING UNDERSTORY PRODUCTION IN SOUTHWESTERN PONDEROSA PINE FORESTS

Although many workers have investigated net annual primary production of understory communities in southwestern ponderosa pine forests (Table 3), all previously reported estimates were based on the peak standing crop. This procedure involves sampling the understory when biomass (standing crop) has reached a seasonal maximum, usually on or about 1 September in Arizona pine forests. One either harvests above-ground biomass on a sample of small quadrats or uses a combination of harvest and estimation. Since the peak standing crop method of determining production does not account for losses to the litter occurring prior to the sampling date or for production occurring after the sampling date, it provides characteristically low estimates of production (Kelly, Van Dyne, and Harris 1974; Tumidajowicz 1973, 1976).

An alternative procedure is to sample biomass at intervals throughout the growing season. Production may be calculated from the seasonal biomass data by several methods. These cumulative procedures provide higher, more realistic estimates of net annual primary production (Kelly et al. 1974). This study employed such a cumulative procedure, called the summation of positive increments. Since this is the first time this procedure has been applied to the determination of understory production in an Arizona ponderosa pine forest, the objective of this study is to further describe the method and to compare it

to the peak standing crop method. Two additional procedures are also presented and evaluated: the peak species biomass method and the summation of July and September biomass. The latter method is a compromise procedure presented herein as a possible alternative for future studies.

Methods

Sampling for biomass was described in the METHODS section in the main body of the dissertation. Production was calculated separately for each plot. The biomass data collected in early September were used as the peak standing crop estimate of production. The peak species biomass estimate was calculated by summing the peak standing crops of individual species. The biomass data collected in July and September were summed to give the summation of July and September biomass estimate of production. The summation of positive increments estimate was obtained by summing by species all increases in biomass from one sampling date to the next. The biomass data collected in May (first sampling date) were used as an estimate of the production for a 4-week period preceding that sampling date. Production of the six sampling intervals was then summed to give the estimate of net annual primary production by summation of positive increments.

Results and Discussion

Since summation of positive increments should be the most accurate method--it utilizes all the data collected throughout the growing season and is not biased by variation in the seasonal patterns

of production among the component species--it is used as the standard for evaluating the other methods.

In this study, summation of positive increments gave the highest estimates of production (Table 9). These values, however, might be biased upward by the possible inclusion of false or apparent increases in biomass. Kelly et al. (1974) suggest testing all biomass increases for statistical significance. Since the power of such tests is low in heterogeneous communities, the application of statistical criteria may have unrealistic and undesirable consequences: (1) elimination of all Type I errors (accepting a false increase in biomass) while retaining all Type II errors (rejecting a true increase in biomass), which would bias the results downward; and (2) assigning zero production to most of the uncommon and rare species in species-rich communities because of their low frequencies and consequently high standard errors.

No such statistical criteria were incorporated here in the calculation of production by summation of positive increments. Overestimation of net annual primary production by harvest techniques is unlikely to occur because harvesting of live biomass fails to account for consumption by herbivores or for losses to the litter occurring between sampling dates. Accuracy could thus be improved by sampling at shorter intervals and by including standing and down litter (Wiegert and McGinnis 1975).

Accuracy and precision of the four methods of determining understory production are compared in Tables 9 and 10. Using summation of positive increments as the standard of comparison, all other methods

Table 9. Comparison of accuracy of methods for determining understory production.

Floristic Group	Means				Percentage Composition			
	Sum Positive Incre- ments	Peak Standing Crop	Peak Species Biomass	Sum July + Sept. Biomass	Sum Positive Incre- ments	Peak Standing Crop	Peak Species Biomass	Sum July + Sept. Biomass
	-----kg/ha/yr-----				-----per cent-----			
Grasses and Sedges	229.6	109.2	138.9	186.8	40.5	45.5	38.9	41.3
Composites	86.4	47.2	50.7	70.1	15.2	19.7	14.5	15.5
Legumes	125.9	38.8	95.3	113.7	22.2	16.2	27.3	25.1
Other Herbs	77.2	34.2	46.3	53.1	13.6	14.3	13.3	11.7
<u>Pteridium aquilinum</u>	48.9	10.8	18.4	28.7	8.6	4.5	5.3	6.3
Total Understory Plants	567.5	240.0	349.4	452.3	100.0	100.0	100.0	100.0
						5.56	2.49	1.28

χ^2

underestimate production (Table 9). The peak standing crop estimate of production is particularly low--only 42% of the value obtained using summation of positive increments. The peak species biomass method and summation of July and September biomass gave estimates of total net annual primary production that were 62% and 80%, respectively, of the value obtained using summation of positive increments.

Table 9 expresses the means of the floristic groups obtained using each method as relative values, i.e., percentages of the respective totals, in order to evaluate the accuracy of the methods in representing species composition. The three alternative procedures are compared to the summation of positive increments method using the χ^2 statistic. Again, the peak standing crop method gave the poorest results, particularly underestimating the percentage composition of legumes and Pteridium. The summation of July and September biomass estimates most closely corresponded to the species composition obtained using summation of positive increments.

Standard errors and coefficients of variation are presented in Table 10 to compare the precision of the four methods. Generally, the higher the estimate of the mean, the higher the standard error of that mean. Comparing the coefficients of variation (the ratios of the standard deviation over the mean expressed as a percentage), the relatively more intensive summation of positive increments method was the most precise. Otherwise, relative precision generally increased from the peak standing crop method to the peak species biomass method to the summation of July and September biomass method. The differences in

Table 10. Comparison of precision of methods for determining understory production.

Floristic Group	Standard Error of the Mean				Coefficient of Variation			
	Sum Positive Incre- ments	Peak Standing Crop	Peak Species Biomass	Sum July + Sept. Biomass	Sum Positive Incre- ments	Peak Standing Crop	Peak Species Biomass	Sum July + Sept. Biomass
	-----kg/ha/yr-----				-----per cent-----			
Grasses and Sedges	38.5	29.0	34.2	43.6	92.0	145.2	134.2	127.9
Composites	11.6	10.5	10.7	12.8	74.2	122.1	115.8	100.2
Legumes	25.0	8.2	22.9	26.0	108.7	115.6	131.8	125.3
Other Herbs	13.8	8.2	9.7	12.0	97.7	131.1	112.6	125.7
<u>Pteridium aquilinum</u>	21.1	8.7	12.9	13.0	236.5	444.8	386.4	248.8
Total Understory Plants	62.8	37.5	54.9	63.6	60.7	85.7	85.6	77.0

relative precision, however, were not great compared to the differences in accuracy.

The peak standing crop method is the least accurate, least precise, and gives the poorest representation of species composition. Unfortunately, it has been the method universally applied to understory communities in southwestern ponderosa pine forests and elsewhere, primarily because it is the most economic method to apply. The poor results obtained by this method can best be explained by the seasonal trends in precipitation, biomass, and production (Figures 1, 3, 4). Total production (Figure 4) showed a distinctly biseasonal trend, reflecting the biseasonal pattern of precipitation on the study site (Figure 1). This biseasonal pattern results in two more or less distinct periods of maximum biological activity, as described in the main body of the text. It is clear from Figure 4 why legumes are most poorly estimated by the peak standing crop method--their peak production is early in the growing season. Only grasses and sedges and composites reach maximum production at the time when peak standing crop estimates are made--in late August or early September.

Figure 3 shows the seasonal trends in biomass. Although the total standing crop did peak in early September, it was relatively high from June to October. Plants and plant parts were continuously dying as new green matter was produced. The steady decline in biomass of legumes after June was particularly evident. At the time when peak standing crop estimates are usually made in late August to early September, only composites were actually at their peak standing crop.

Note in Figure 3 that all four floristic groups on the study site reached maximum biomass at different times. Each group, of course, is composed of a number of species, each with somewhat different seasonal trends in biomass and production. Such temporal partitioning of a biseasonally favorable environment explains the relatively high values of production found using summation of positive increments--it is the only procedure of the four that can realistically account for such seasonal differences.

In addition to providing the most accurate and most precise estimates of understory net annual primary production, summation of positive increments is the only appropriate method if seasonal trends in production are desired. There are two major practical problems with the method, however: (1) it requires time consuming sampling at intervals throughout the growing season; and (2) it imposes severe demands on the taxonomic expertise of the investigator, particularly in diverse communities. All harvested material must be identified to species at all phenological stages. For this study, keys were developed to identify juvenile grasses and sedges and rosette herbs, the most difficult groups to distinguish vegetatively.

Peak species biomass estimates also require sampling at several dates in the growing season and precise species identification. The peak species biomass estimates of production were also low, relatively imprecise, did not show seasonal trends in production, and did not provide a good representation of species composition. This method is usefull when biomass is sampled at two or more times in the growing

season, but sample data are not available for a complete growing season. In such situations, the peak species biomass method may provide the best available estimate of production.

The method of summation of July and September biomass is proposed herein as a compromise of accuracy and efficiency in this community type. This estimate was obtained by summing the biomass data collected during the early July and early September sampling periods. The July biomass data approximates a peak standing crop estimate for the spring season. Likewise, the September biomass data provides an estimate of the summer season peak standing crop; summing the two provides an estimate of net annual primary production. This method was considerably more accurate, somewhat more precise, and provided a better representation of species composition than the peak standing crop. It requires sampling at two times, but is considerably less time consuming than the sampling required by the method of summation of positive increments. It requires the same relatively low level of taxonomic expertise as the peak standing crop method. Dominant and easily recognizable species can be treated separately, rare and unknown species can be pooled as desired without affecting the estimate of total net annual primary production.

APPENDIX D

EFFECTS OF CONTROLLED BURNING ON UNDERSTORY PRODUCTION, CANOPY, LITTER, AND SOILS IN AN ARIZONA PONDEROSA PINE FOREST

Data for this study was collected as part of a study of the effects of controlled burning on ponderosa pine forest understory communities. The objective of this study was to describe the effects of that burning on the understory plants and on the environmental attributes that may influence those plants.

Methods

The control burn on the study site was carried out in conjunction with Bureau of Indian Affairs personnel on 29 October 1975, starting at 1400 hours and continuing into the night. Afternoon temperature and humidity were 15 °C and 35%; early morning temperature and humidity were 0 °C and 55%. Winds were light and variable. In most of the study area the fire was a low creeping ground fire with only a few local hot spots. Fire intensity was generally low and rate of spread was slow. One predesignated member of each plot pair received the burning treatment.

Transmissivity, O1 litter, O2 litter, total soil nitrogen, soil organic matter, nitrate, phosphate, calcium, magnesium, potassium, sodium, and pH were determined before and after the burn. Biomass of understory plants was sampled on three dates before the burn--once

each in June, July, and August. All environmental attributes were sampled on three quadrats per plot. Other details of the sampling and methods of determination are described in the main body of the dissertation.

Fire effects were evaluated using paired t-tests, pairing the control and burn plot pair members. The data collected prior to burning showed that there were no significant pre-treatment differences in understory biomass between plots designated for burn and control treatments. A more complex t-test was required for the environmental attributes, since there was an initial difference in soil nitrate ($p < .05$) between burn and control plots, and there was considerable deviation in the data supplied by the soils lab for the two years. For the environmental attributes, differences due to burning were calculated as:

$$\bar{D}_j = \frac{\sum_{i=1}^{15} (A(1976)_i - A(1975)_i) - (B(1976)_i - B(1975)_i)}{15}$$

where: \bar{D}_j = mean difference in attribute j due to burning

$A(1976)_i$ = value of attribute j on burn plot i after burning

$A(1975)_i$ = value of attribute j on burn plot i before burning

$B(1976)_i$ = value of attribute j on control plot i after burning

$B(1975)_i$ = value of attribute j on control plot i before burning

and:

$$t = \frac{\bar{D}_j}{S.E.(\bar{D}_j)}$$

where: $S.E.(\bar{D}_j)$ = the standard error of \bar{D}_j

This analysis compares burn and control plots correcting both for any

differences between years, either actual differences or differences in the determination of the attributes, and for any initial differences between members of the paired plots, allowing for a reliable identification of burning effects.

Results and Discussion

The effects of burning on the canopy, litter, and soil attributes investigated are shown in Table 11. Only the O1 litter layer was significantly altered by the fire. The O2 litter showed a slight but non-significant increase, probably due to the addition of ash from the O1 layer. Transmissivity was unchanged. Non-significant decreases were recorded for total nitrogen and nitrate. Organic matter, phosphate, pH, and all soil cations showed non-significant increases. These results supported the visual impressions of low fire intensity--more intensive burning treatments in ponderosa pine are known to have greater effects on these soil and litter attributes (Vlamis, Biswell, and Schultz 1955; Fuller, Shannon, and Burgess 1955; Sweeney and Biswell 1961; Klemmedson et al. 1962).

The effects of burning on understory production on the 15 plot pairs in ponderosa pine are summarized in Table 12, which presents the means, standard errors, and standard errors of the difference of the net annual primary production for common and abundant species on the burn and control plots. The large standard errors of these estimates are associated with the diversity of stands sampled. Paired t-tests showed no significant differences in production between control and burn plots. Over the entire growing season, control and burn plots

Table 11. The effects of controlled burning on canopy, litter, and soil variables on the fifteen ponderosa pine plot pairs.

Attributes, units	\bar{D}_j
Transmissivity (per cent east-south-west canopy open)	0.2 n.s. ^a
O1 Litter (tons/ha)	-2.24 p<0.1
O2 Litter (tons/ha)	1.11 n.s.
Organic Matter (per cent)	.77 n.s.
Total Nitrogen (ppm)	-35 n.s.
pH	.07 n.s.
Nitrate (ppm)	-6.4 n.s.
Phosphate (ppm)	.02 n.s.
Calcium (meq/100 gm soil)	.26 n.s.
Magnesium (meq/100 gm soil)	.06 n.s.
Sodium (meq/100 gm soil)	.02 n.s.
Potassium (meq/100 gm soil)	.03 n.s.

^anot significant

Table 12. Understory net annual primary production on burn and control plots.

Taxon	Burn		Control		Standard Error of Difference
	Mean	S.E.	Mean	S.E.	
	-----kg/ha/yr-----				
Total Understory Plants	574.2	+ 85.2	560.8	+ 95.4	72.1
Grasses and Sedges	220.0	+ 54.1	236.3	+ 56.7	23.7
Composites	89.3	+ 17.1	83.3	+ 16.5	19.6
Legumes	121.6	+ 35.2	130.0	+ 36.6	20.4
Other Herbs	78.1	+ 16.7	76.3	+ 22.5	34.8
<u>Carex geophila</u>	20.4	+ 7.4	18.5	+ 6.0	7.4
<u>Koeleria cristata</u>	6.3	+ 1.6	6.6	+ 2.5	2.5
<u>Muhlenbergia virescens</u>	18.0	+ 5.7	40.1	+ 17.9	16.3
<u>Poa fendleriana</u>	55.7	+ 14.4	58.5	+ 10.3	8.2
<u>Poa pratensis</u>	64.6	+ 50.5	60.9	+ 46.4	4.5
<u>Sitanion hystrix</u>	46.3	+ 12.5	38.6	+ 5.2	8.7
<u>Achillea lanulosa</u>	32.6	+ 16.9	17.5	+ 5.4	13.7
<u>Cirsium wheeleri</u>	8.2	+ 2.9	9.0	+ 2.6	3.2
<u>Erigeron formosissimus</u>	24.2	+ 6.6	38.0	+ 12.7	11.8
<u>Senecio neomexicanus</u>	3.0	+ 1.0	7.3	+ 2.2	1.4
<u>Trifolium rusbyi</u>	103.0	+ 35.4	99.9	+ 36.7	19.7
<u>Vicia americana</u>	5.8	+ 2.0	11.9	+ 3.5	3.1
<u>Pseudocymopterus montanus</u>	10.8	+ 2.9	12.1	+ 2.9	2.9
<u>Rosa arizonica</u>	24.3	+ 7.6	22.3	+ 7.8	6.1
<u>Pteridium aquilinum</u>	65.2	+ 38.5	38.1	+ 22.1	34.8

were nearly identical in both net annual primary production and species composition.

Why didn't the fire have a significant effect on understory production? The only significant effect of the burn was a decrease in the O1 litter layer--other important site characteristics, such as canopy cover, O2 litter, and soil variables were not altered (Table 11) by this low intensity burn. Data presented in the main body of the dissertation showed that O1 litter was not a significant factor in the distribution of most understory species. Light ground fires that reduce or remove only the uppermost litter do not alter the environment sufficiently to change understory production or alter species composition.

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