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Changes in Ponderosa Pine Site Productivity following Removal of Understory Vegetation

M. D. Busse, * P. H. Cochran, and J. W. Barrett

ABSTRACT

Competition from understory vegetation for water and nutrients can limit productivity of young forest stands. Less is known of the effect of understory vegetation on long-term stand growth or soil organic properties. The effect of understory vegetation on periodic annual increments (PAIs) of basal area, height, and volume for ponderosa pine (*Pinus ponderosa* Dougl.) in central Oregon at 4 or 5-yr intervals was examined for a 35-yr period. Soil C, N, and microbial biomass C (MBC) were also quantified after 32 and 35 yr with and without understory vegetation on a sandy loam pumice soil (Xeric Vitricryand). Five tree spacings, ranging from 2.0 to 8.0 m (154-2469 trees ha⁻¹), in combination with two understory treatments (understory vegetation present or continuously absent) were installed in 1959. Total understory vegetation cover averaged 3570 between 1959 and 1994 for treatments with understory vegetation present, and was dominated by three shrub species: antelope bitterbrush [*Purshia tridentata* (Pursh) DC.], greenleaf manzanita (*Arctostaphylos patula* Green), and snowbrush (*Ceanothus velutinus* Dougl. ex Hook.). Covariance analyses of PAIs for each successive interval were performed using appropriate stand parameters at the start of each interval as covariates. Tree growth was reduced by competing understory vegetation during the first 12 to 20 yr only; understory vegetation did not reduce the adjusted PAIs during the last 15 yr. Soil C and N were measured incrementally to a depth of 24 cm. Presence of understory vegetation resulted in greater C and N in the O horizon and upper 4 to 12 cm of mineral soil. Seasonal MBC, measured at 14-d intervals from May to November, was greater when understory vegetation was present. The results suggest that understory vegetation plays an important role in maintaining soil quality.

WILDFIRE SUPPRESSION began shortly after the turn of the century in ponderosa pine forests of central Oregon. Prior to that time, most stands experienced light, periodic ground fires (Bork, 1985), effectively controlling the understory vegetation and creating open, shrub-depauperate conditions. By the 1940s, the absence of fire resulted in stands with a dense understory of suppressed pine and a well-developed shrub component consisting primarily of antelope bitterbrush, greenleaf manzanita, and snowbrush. This large-scale change in stand structure and understory vegetation composition sparked concern for the potential reduction in tree vigor and growth due to increased competition for soil water (Van Sickle and Hickman, 1959) and nutrients.

Competition from understory vegetation retards the early development of ponderosa pine (Barrett, 1982; Oliver, 1990; Oren et al., 1987). Barrett (1982) reported large reductions in height and diameter growth of pine saplings when a natural understory was allowed to develop, and Oliver (1990) found similar losses in volume due to understory shrubs in a 20-yr-old plantation. The complexity of factors responsible for these growth de-

clines was not clearly defined in either study, yet limitations caused by increased competition for water and nutrients are implicit (Barrett and Youngberg, 1965; Riegel et al., 1991, 1992; Nambiar and Sands, 1993).

Contrary to their role as competitors for soil resources, shrub species common to central Oregon may enhance long-term site productivity by their ability to supply fixed C and N. Both snowbrush and bitterbrush are actinorhizal shrubs, capable of fixing atmospheric N₂ in symbiosis with species of the soil bacteria *Frankia* (Delwiche et al., 1965; Webster et al., 1967). Nitrogen accretion of about 100 kg ha⁻¹ yr⁻¹ has been credited to snowbrush in mixed conifer stands in the Oregon Cascades (Youngberg and Wollum, 1976; McNabb and Cromack, 1983). Less is known of N₂-fixing potential of bitterbrush, although its inconsistency in modulation (Righetti and Munns, 1982) and low nitrogenase activity (Dalton and Zobell, 1977) suggest a minor role in site N accretion.

A long-term study was established at the Pringle Falls Experimental Forest in 1959 to answer three questions: (i) Can suppressed ponderosa pine saplings develop into crop trees when released by overstory removal and thinning? (ii) How do tree and stand growth rates vary with tree spacing? (iii) How does the shrub-dominated understory vegetation influence development of thinned, second-growth stands? We examined the effect of understory vegetation on growth of ponderosa pine during a 35-yr period at Pringle Falls and report differences in soil N, C, and microbial biomass C due to the presence of understory vegetation.

MATERIALS AND METHODS

Site Description

The study area (43°44'N, 121°36'W; 1340 m elevation) is 56 km southwest of Bend, OR, in the Pringle Falls Experimental Forest. Average slope is 10% (ranging from 4 to 27%) and the aspect is predominantly east facing (ranging from 14 to 1670). Mean annual precipitation of 61 cm falls mainly from October through April, with a 60-cm snowpack common between January and March. Maximum average temperature in July is 25.5°C and frosts can occur in any month.

The soil, a Xeric Vitricryand, is developing on 84 cm of dacite pumice from the eruption of Mount Mazama (Crater Lake) about 7800 yr ago (Bacon, 1983). The pumice mantle overlies a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments. The texture of the A (0-5-cm depth) and AC (5-36-cm depth) horizons is loamy coarse sand, the texture of the C 1 horizon (36-63-cm depth) is single-grained, coarse gravelly sand, and the texture of the C2 horizon (63-84 cm) is single-grained, coarse and very coarse pumice sand. Soil pH varies from 5.7 to 6.2 for the A horizon and from 6.0 to 6.5 for the other pumice horizons. Site index for ponderosa pine is 24 m (Meyer, 1961).

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Abbreviations: PAI, periodic annual increment; MBC, microbial biomass carbon; TPH, trees per hectare; QMD, quadratic mean diameter; SE, standard error of the mean.

Before the study was installed, the stand consisted of old-growth ponderosa pine with an average of 49 trees ha⁻¹, a mean tree diameter of 65 cm, and an understory of 40- to 70-yr-old suppressed ponderosa pine saplings. Average diameter of the understory trees was 2.5 cm, average height was 2.4 m, and the density was 17284 stems ha⁻¹. Shrub and herbaceous vegetation consisted of antelope bitterbrush, snowbrush, and greenleaf manzanita, with scattered Ross sedge (*Carex rossi* Bott), western needle grass (*Stipa occidentalis* Trub. ex Wats.), and bottlebrush squirreltail [*Sitanion hystrix* (Nutt.) J.G. Smith].

Experimental Design and Measurements

There are 30, 0.078-ha plots distributed across 65 ha. Each 24.1 by 32.2 m plot is surrounded by a 10-m buffer strip. Six replications of five tree spacings were randomly assigned: 2.0 m (2469 trees ha⁻¹ [TPH]), 2.8 m (1235 TPH), 4.0 m (617 TPH), 5.7 m (309 TPH), and 8.0 m (154 TPH). Logging of all overstory and thinning of remaining saplings was completed in the fall of 1958. All logging and thinning slash was removed from the plots and burned. All understory vegetation was removed in the spring of 1959 and at successive 3- to 4-yr intervals on three randomly chosen replications per tree spacing and allowed to develop naturally on the three remaining replications. Manual control and 2,4,5-T [(2,4,5-trichlorophenoxy) acetic acid] were used in the initial removal of understory vegetation; manual control and 2,4,-D [(2,4-dichlorophenoxy) acetic acid] were used in the following two removals; manual control alone has been used since. The design is a completely randomized, 5 x 2 factorial with three replications, and becomes a split plot in time for analysis of growth rates and understory cover during different growth periods.

Diameter and total height of all trees were measured in the fall of 1959, 1963, 1967, 1971, 1975, 1979, 1984, 1989, and 1994. Diameters were measured to the nearest 0.25 cm with a steel tape and heights were measured to the nearest 0.15 m with sectioned aluminum poles or optical dendrometers. Tree volumes were calculated using an equation for second-growth ponderosa pine developed by DeMars and Barrett (1987). Periodic annual increment (growth divided by the number of growing seasons per period) for gross basal area, gross volume, and height of surviving trees was determined for each of the eight periods.

Understory vegetation cover was measured by systematic sampling of 100 points per plot (Heady et al., 1959) in 1959, 1963, 1967, 1971, 1979, and 1994 on understory-vegetation-present treatments. Aboveground biomass of understory shrubs was estimated in 1994 using equations developed for central Oregon ponderosa pine stands (Means et al., 1994). Canopy area and stem diameter (manzanita only) were measured on all shrubs within three 84.4-m² subplots to determine aboveground biomass using the predictive equations. Aboveground biomass of herbaceous plants was not determined.

Organic C and total N of the mineral soil were determined for the 0- to 4-, 4- to 8-, 8- to 12-, and 12- to 24-cm depths in the summer of 1994. Samples (<2 mm) were composites from 20 subsample cores taken systematically across each plot. Carbon and N concentrations were determined using a C analyzer (NA 1500, Carlo Erba, Milan, Italy) and were converted to total content per hectare by multiplying by the respective bulk density (average of three replications) of each plot and depth.

Depth of the O horizon was measured systematically at 40 points per plot. No attempt was made to separate the Oi, Oa, and Oe horizons because of their poor delineation at this site and the high degree of subjectivity of this measurement

(Federer, 1982). Bulk density was estimated from 10 subsamples per plot using 10-cm-diam. cores. Depth and bulk density were used to calculate O horizon dry mass per hectare. Carbon concentration was determined using the same method listed for mineral soil. Total N was determined with a continuous flow analyzer following Kjeldahl digestion (Bremner and Mulvaney, 1982).

Microbial biomass C was determined by the chloroform-fumigation-incubation method (Jenkinson and Powlson, 1976) on samples collected in May of 1991 from 0- to 2-, 2- to 4-, and 4- to 8-cm depths. Subsequently, measurements were taken at 14-d intervals throughout the summer and fall on samples from the 0- to 2-cm depth. Samples (25 g dry wt., <6 mm) were composite from 10 random subsamples and analyzed within 24 h of collection. Moisture contents were determined and samples were analyzed for MBC at their field moisture content. Following a 24-h incubation with CHCl₃, samples were inoculated with 0.7 g of nonsterile soil and incubated at 21°C for 10 d in 0.5-L vessels containing 0.5 M NaOH traps. Biomass C was calculated by the difference between CO₂ evolved from fumigated and nonfumigated (0- 10d incubation) soil, using a proportion factor (*k*) of 0.41 (Anderson and Domsch, 1978).

A pandora moth (*Coloradia pandora* Blake) outbreak began in the study area in 1991. Partial defoliation occurred in 1992 and 1994. Percentage defoliation for each plot was estimated by examining tree crowns with binoculars.

Statistical Analysis

Repeated measures analyses (SAS Institute, 1988) were used to test the following hypotheses: (i) understory vegetation cover did not change with TPH or period; (ii) gross basal area PAI, survivor height PAI, and gross volume PAI did not change with understory vegetation treatment, TPH, or period; (iii) diameter and height of live trees did not change with understory vegetation treatment, TPH, or period; (iv) seasonal microbial biomass C did not change with understory vegetation treatment or TPH. Although the periods were not equal in length (five 4-yr periods and three 5-yr periods), the differences were considered too small to warrant weighting in the repeated measures analyses. Repeated measures analysis was also used to test the effect of understory vegetation on percentage defoliation by pandora moth in 1992 and 1994. Analysis of variance with soil depth, as a split plot, was used to test the effect of understory vegetation, TPH, and depth on soil C, N, C/N, and MBC. Linear, quadratic, cubic, and quartic effects for TPH and depth were tested when appropriate using orthogonal polynomial methods. Unequal intervals for TPH were taken into account in determining the coefficients (Bliss, 1970). The significance level for all comparisons was *P* < 0.05.

Because PAIs are functions of site, tree age, and stand density, they can be affected during a long-term study both directly by the treatment and indirectly by differences in stand density and tree size that develop as a result of treatment (Miller and Tarrant, 1983; Auchmoody, 1985). Two procedures were used to separate the direct (treatment) and indirect (stand density) effect of understory vegetation of PAIs. First, PAIs for each period were plotted as a function of the basal area or volume at the start of the period. Second, analysis of covariance was used, separately by period, to test the effect of understory vegetation at similar stand densities or similar stand densities and tree heights. Separate analyses of covariance were used for each period instead of a combined model because variances for each PAI and regression coefficients for the covariates differed between periods. Basal area (BA) at the start of each period and BA² were used as covariates for

analysis of basal area PAI. Average height at the start of each period and BA were used as covariates for analysis of height PAI. Volume (V) at the start of each period and V^2 were used as covariates in the analysis of volume PAI. These covariates were derived from studies documenting relations between tree growth and density (Miller and Tarrant, 1983; Ronco et al., 1985; Oliver and Edminster, 1988).

RESULTS

Understory Vegetation Cover and Shrub Biomass

Total understory vegetation cover for treatments with understory present averaged 35% (28 % shrubs, 7 % herbaceous plants) between 1959 and 1994. Cover was lowest in 1959, 1 yr after logging and thinning operations were completed, and relatively low again in 1979 following severe winter kill in 1976–1977 (Table 1). Bitterbrush was the most abundant shrub species at every sampling date. Cover of herbaceous plants increased between 1959 and 1967, and has since steadily declined to become a minor component of the understory. Manzanita and total shrub cover decreased with increasing TPH, while neither bitterbrush nor snowbrush cover were significantly related to TPH. Aboveground biomass of shrubs, mea-

Table 1. Percentage canopy cover of bitterbrush, manzanita, *Ceanothus*, and herbaceous plants for understory-vegetation-present treatments between 1959 and 1994 as a function of trees per hectare (TPH).

TPH	1959	1963	1967	1971	1979	1994
no. ha ⁻¹	%					
	<u>Bitterbrush cover</u>					
154	15	20	17	21	11	15
309	13	16	19	20	11	19
617	14	17	22	22	17	17
1235	12	18	16	13	13	17
2469	6	10	12	18	12	8
	<u>Manzanita cover</u>					
154	7	7	6	7	14	17
309	3	1	0	2	6	18
617	5	2	2	5	6	8
1235	4	1	1	3	4	3
2469	2	2	2	3	3	4
	<u>Ceanothus cover</u>					
154	6	7	8	13	8	6
309	7	12	13	12	7	8
617	4	4	4	7	5	5
1235	6	11	11	10	6	5
2469	5	11	6	12	10	2
	<u>Total shrub cover</u>					
154	28	34	32	41	33	38
309	23	29	32	34	24	45
617	22	22	28	34	27	30
1235	20	29	28	26	22	26
2469	12	23	21	33	25	13
	<u>Herbaceous cover</u>					
154	5	11	10	7	3	3
309	5	14	15	13	6	5
617	3	13	12	7	3	2
1235	5	10	11	9	1	1
2469	5	7	8	2	1	2
	<u>Total cover</u>					
154	33	45	43	48	35	41
309	29	43	47	47	29	50
617	26	35	40	41	30	32
1235	26	39	39	35	24	27
2469	18	30	29	35	26	15

sured in 1994, followed similar trends to that of shrub cover (Table 2). Manzanita biomass declined linearly and total shrub biomass declined curvilinearly with increasing TPH, whereas bitterbrush and snowbrush biomass were not affected by TPH.

Tree Size, Mortality, and Periodic Annual Increments

Quadratic mean diameter averaged 5.2 cm and average height was 3.6 m for all treatments at the start of the study. The QMDs and average heights increased curvilinearly with decreasing TPH and became larger for each TPH in the absence of understory vegetation as the study progressed. After 30 yr, average QMDs were 14.1, 17.4, 21.7, 26.9, and 30.7 cm for the narrowest to widest spacings, respectively, where understory vegetation was present. Corresponding average heights were 9.0, 9.5, 11.2, 12.9, and 13.7 m. For the narrowest to widest spacings with understory vegetation absent, QMDs averaged 14.6, 18.2, 23.9, 29.9, and 36.8 cm while heights averaged 9.0, 10.3, 12.4, 14.4, and 15.0 m.

Tree mortality was minimal during the 35-yr study. Only 1.6% of all trees died, confined to the three highest TPH treatments. Trees lost to mortality were small; their mean diameter was 50% of the mean diameter of all trees on a given plot at the start of a period. As a result, differences between gross and net PAIs for any plot in any period were never >5 %, and averaged <1% for both basal area and volume PAI.

Volume PAI was greater in the absence of understory vegetation for the 35-yr period (Fig. 1, Table 3). Basal area and height PAIs also showed the same response between treatments (data not shown). A curvilinear increase in volume PAI was found with increasing TPH. Volume PAI did not vary consistently with TPH during each period, however, resulting in a significant period x TPH interaction. Maximum growth rates occurred primarily at or before the sixth growth period. Growth rates were low in the eighth period because of partial defoliation by pandora moth in 1992 and 1994. Defoliation did not differ with the presence or absence of understory vegetation.

The effect of understory vegetation on volume PAI changed with period as shown by the significant period x understory vegetation interaction (Table 3). Plotting

Table 2. Effect of overstory treatment (trees per hectare, TPH) on aboveground biomass of shrub species in 1994.

TPH	Bitterbrush	Manzanita	<i>Ceanothus</i>	Total
no. ha ⁻¹	kg ha ⁻¹			
154	635	1938	647	3221
309	740	1969	630	3339
617	1051	925	613	2589
1235	837	524	697	2057
2469	435	435	207	1071
	<u>Orthogonal comparisons, $P > F$</u>			
linear	- †	0.0144		0.0247
quadratic		0.1688		0.0747
cubic		0.5382		0.5977
quartic		0.9745		0.6155
CV, %	46.4	66.5	82.5	38.7

† Main effect of TPH not significant at $P < 0.05$.

volume PAI as a function of volume at the start of a period indicates a clear change in understory vegetation treatment response between the first and seventh period (Fig. 2). Plotting basal area PAI vs. basal area at the start of the period showed a similar change in response to understory vegetation treatment between the first and seventh period. Covariance analyses for individual periods also showed that the direct effect of the understory vegetation on PAIs changed during the 35 yr of observation (Table 4). Adjusted means for PAIs were greater for treatments with understory vegetation absent than treatments with understory vegetation present only in the first three to five periods (12–20 yr).

Soil Carbon, Nitrogen, and Microbial Biomass Carbon

Carbon content in the upper 24 cm of mineral soil averaged 23.5 Mg ha⁻¹ for treatments with understory vegetation and 18.8 Mg ha⁻¹ for those without understory vegetation (Table 5). The largest differences between treatments were found in the upper 12 cm. Continuous absence of understory vegetation resulted in 33% lower C in the 0- to 4-cm depth, 11% lower C in the 4- to 8-cm depth, and 10% lower C in the 8- to 12-cm depth. No differences were found below 12 cm, resulting in a significant understory vegetation x depth interaction

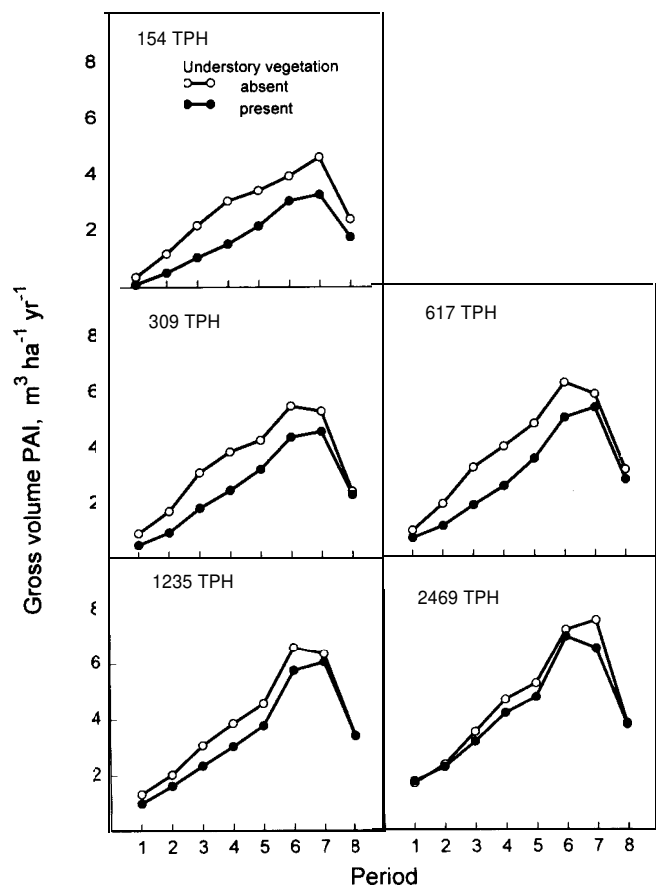


Fig. 1. Gross volume periodic annual increment (PAI) with and without understory vegetation for each trees per hectare (TPH) treatment during consecutive 4- or 5-yr period; between 1960 and 1994.

Table 3. Repeated measures analysis of variance *P* > *F* values for the effect of trees per hectare (TPH), understory vegetation (V), and growth period (P) on volume periodic annual increment (PAI).

Source	df	<i>P</i> > <i>F</i>
Whole plot		
TPH		
linear	1	0.0001
quadratic	1	0.0332
cubic	1	0.0955
quartic	1	0.1648
V	1	0.0001
TPH x V	4	0.5188
Sub plot		
P	7	0.0001
P x TPH		
linear	7	0.0001
quadratic	7	0.0823
cubic	7	0.2048
quartic	7	0.5793
P x V	7	0.0001
P x T P H x V	28	0.8939
<u>Error mean square</u>		
whole plot		1.122
subplot		0.099

(Table 6). A significant TPH x depth x vegetation interaction resulted from the inconsistent effect of TPH on soil C with increasing soil depth.

Total N in the upper 24 cm of mineral soil averaged 874 kg ha⁻¹ for treatments with understory vegetation and 737 kg ha⁻¹ for treatments without understory vegetation (Table 5). Nitrogen content was 30% lower in the upper 4 cm when understory vegetation was absent. No treatment differences were found below 4 cm, resulting in a significant understory vegetation x depth interaction (Table 6). Carbon/nitrogen ratios were generally higher

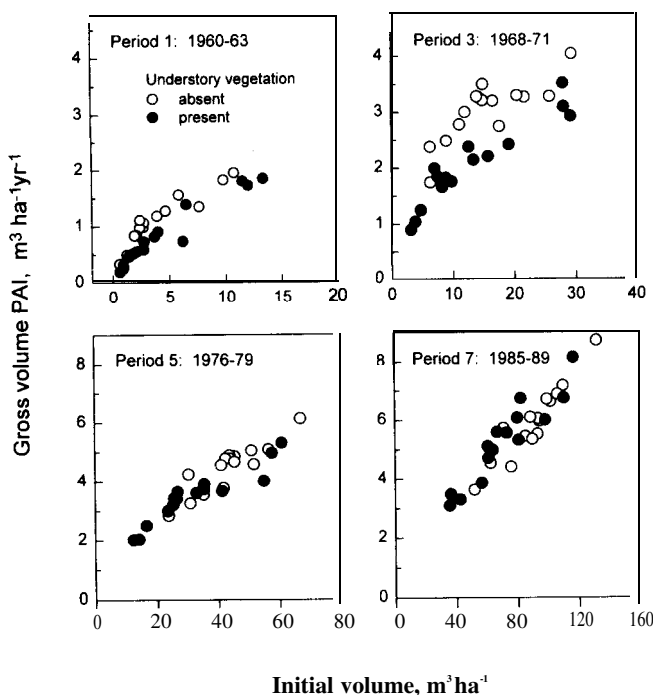


Fig. 2. Gross volume periodic annual increment (PAI) as a function of volume at the start of periods 1, 3, 5, and 7.

Table 4. Analysis of covariance adjusted means and *P* values for basal area, height, and volume periodic annual increments (PAI) during eight consecutive growth periods between 1960 and 1994.

Period	Basal area PAI			Height PAI			Volume PAI		
	Understory absent	Understory present	<i>P</i> > <i>T</i>	Understory absent	Understory present	<i>P</i> > <i>T</i>	Understory absent	Understory present	<i>P</i> > <i>T</i>
	m ² ha ⁻¹ yr ⁻¹			m yr ⁻¹			m ³ h a ⁻¹ y r ⁻¹		
1 (1960-1963)	0.57	0.41	0.0001	0.11	0.08	0.0019	1.10	0.83	0.0001
2 (1964-1967)	0.76	0.61	0.0001	0.22	0.14	0.0001	1.81	1.35	0.0001
3 (1968-1971)	0.92	0.75	0.0001	0.37	0.27	0.0001	2.89	2.20	0.0001
4 (1972-1975)	0.93	0.88	0.1330	0.32	0.26	0.0004	3.65	3.00	0.0001
5 (1976-1979)	0.84	0.87	0.3803	0.33	0.32	0.6769	4.13	3.84	0.0666
6 (1980-1984)	0.90	0.96	0.1184	0.35	0.34	0.7165	5.29	5.52	0.3124
7 (1985-1989)	0.77	0.84	0.0116	0.31	0.32	0.5623	5.47	5.78	0.0895
8 (1990-1994)	0.26	0.32	0.0026	0.16	0.16	0.8713	2.76	3.09	0.0319

for treatments with understory vegetation, particularly in the 8- to 12-cm depth.

Average depth (SE) of the O horizon was 4.9 (0.2) cm for treatments with understory vegetation and 4.0 (0.2) cm for treatments without understory vegetation, which corresponds to 21% lower total C ha⁻¹ and 32% lower total N ha⁻¹ without understory vegetation (Table 7). This response was not consistent for all TPHs however; C and N content of the O horizon was greater at 617 TPH in the absence of understory vegetation. As a result, the understory vegetation X TPH interaction was significant for N and tended toward significance for C/N. An increase in C content in the O horizon was also found with increasing TPH.

Microbial biomass C in the upper 4 cm of mineral soil was 19% higher when understory vegetation was present (Table 8). No differences were found below 4 cm, again resulting in a significant understory vegetation X depth interaction. Treatments with understory vegetation had higher (*P* < 0.05) MBC than treatments without understory vegetation on eight out of 10 samples dates throughout the summer and fall in the 0- to 2-cm

depth (Fig. 3). There were no treatment differences for 15 July and 1 Aug. samples, resulting in a significant understory vegetation x sampling date interaction in repeated measures analysis. Seasonal variation in MBC was significantly related to changes in soil water content (*r*² = 0.90 for treatments with understory vegetation, *r*² = 0.82 for treatments without understory vegetation). It is unlikely that the differences between understory vegetation treatments were related to soil water content, however, because both treatments had virtually identical water contents at the 0- to 2-cm depth throughout the season.

DISCUSSION

Previous results from the Pringle Falls study showed that basal area, height, volume, and leaf area index declined in the presence of understory vegetation (Barrett, 1982; Oren et al., 1987). Soil water use, measured in the first 4 yr only, was 45% greater when understory vegetation was present (Barrett and Youngberg, 1965). These past results conform with other short-term studies

Table 5. Total soil C, N, and C/N at different depths after 35 yr of overstory treatment (trees per hectare, TPH) in the absence or presence of understory vegetation.

Soil depth	TPH	C		N		C/N	
		absent	present	absent	present	absent	present
cm	no. ha ⁻¹	Mg ha ⁻¹		kg ha ⁻¹			
0-4	154	6.3	7.7	232	264	27.4	28.9
	309	5.9	9.3	202	348	28.9	26.8
	617	7.1	9.3	249	315	28.4	29.8
	1235	6.3	11.9	220	401	29.0	29.6
	2469	7.6	11.1	266	350	28.4	31.5
	avg.	6.6	9.9	234	336	28.4	29.3
	4-8	154	4.2	5.4	151	201	27.8
309		4.9	4.6	177	172	27.6	26.8
617		5.3	4.8	192	178	27.5	27.0
1235		4.7	6.1	168	219	28.2	28.0
2469		4.3	5.7	161	190	26.8	29.8
avg.		4.7	5.3	169	192	27.6	27.6
8-12		154	2.4	3.5	105	143	23.2
	309	3.6	3.2	138	121	25.6	26.6
	617	2.7	2.9	107	114	25.5	25.7
	1235	3.0	3.1	110	105	26.9	29.1
	2469	2.8	3.3	99	108	28.1	30.7
	avg.	2.9	3.2	112	118	25.8	27.3
	12-24	154	4.4	5.1	212	241	20.6
309		5.5	5.2	241	239	22.7	21.7
617		5.5	3.9	239	185	22.1	21.3
1235		4.8	5.4	206	230	23.2	23.2
2469		4.7	6.1	214	239	22.2	25.6
avg.		5.0	5.1	222	228	22.4	22.6

Table 6. Analysis of variance $P > F$ values for the effects of understory vegetation (V), trees per hectare (TPH), and depth (D) on soil C, N, and C/N.

Source	$P > F$		
	C	N	C/N
Whole plot			
TPH	0.3536	0.8362	0.0011
V	0.0009	0.0010	0.0940
TPH X V	0.2790	0.3514	0.0545
Sub plot			
D	0.0001	0.0001	0.0001
D X TPH	0.0041	0.0041	0.0054
D x V	0.0001	0.0001	0.0586
D x TPH x V	0.0059	0.0003	0.2208
	<u>Error mean square</u>		
whole plot	2.311	2243	4.388
subplot	0.500	570	1.276

which have established that understory vegetation reduces growth rates and negatively affects water relations of conifer seedlings and saplings (Lanini and Radosevich, 1986; Petersen et al., 1988; Coates et al., 1991; Conard and Sparks, 1993).

Our results extend the findings of the earlier Pringle Falls study an additional 15 yr and show an unexpected, temporal change in ponderosa pine growth in response to understory vegetation treatment. The large differences in tree growth between understory vegetation treatments for the initial 20 yr disappeared during the last 15 yr of study when PAIs are adjusted using appropriate stand parameters at the start of each period in covariance analyses. A simple explanation would suggest that growth differences disappeared as a result of increased stand density leading to suppression of understory vegetation. We discount this explanation, however, because a decline in understory vegetation cover between 1959 and 1994 was found only at the narrowest spacing (Table 1).

Both soil water and nutrients limit plant growth in the xeric climatic regime of central Oregon (Barrett and Youngberg, 1965; Cochran, 1978, 1979; Will and Youngberg, 1978; Cochran et al., 1990). The initial increases in tree growth in the absence of understory vegetation, attributed to greater soil water availability, resulted in increased uptake and sequestration of soil nutrients. We speculate that subsequent changes in soil nutrient content and availability counterbalanced differences in water

Table 8. Microbial biomass C (MBC) at different mineral soil depths after 32 yr of overstory treatment (trees per hectare, TPH) in the absence or presence of understory vegetation (V).

Depth	TPH	MBC	
		absent	present
cm	no. ha ⁻¹	<u>mg kg⁻¹</u>	
0-2	154	608	896
	617	803	1020
	2469	893	1086
	avg.	768	1001
2-4	154	714	856
	617	716	771
	2469	730	879
	avg.	720	835
4-8	154	529	553
	617	612	624
	2469	767	716
	avg.	631	637
<u>Analysis of variance, $P > F$</u>			
Whole plot			
TPH			0.0087
V			0.0067
TPH X V			0.6156
Subplot			
depth (D)			0.0001
D X TPH			0.1343
D x V			0.0113
D X TPH x V			0.7650
			<u>Error mean square</u>
whole plot			14483
subplot			11821

availability and potentially contributed to the similar rates of tree growth at comparable densities during the last 15 yr of measurement. For example, by 1994 we found an increase in C in the upper 12 cm of mineral soil, an increase in N and MBC in the upper 4 cm of mineral soil, and an increase in C and N contents in the O horizon in the presence of understory vegetation. Further investigation is required to verify this hypothesis.

Changes in mineral soil C due to management practices have not been well characterized in forest ecosystems. Most studies have examined the C content of the O horizon and its response to harvesting (Covington, 1981; Johnson et al., 1991), or have compared mineral soil C content in forested stands with adjacent shrub stands (Johnson, 1995). Our results provide evidence of long-term changes in mineral soil C and indicate the role of

Table 7. Mean C, N, and C/N of the O horizon after 35 yr of overstory treatment (trees per hectare, TPH) in the absence or presence of understory vegetation (V).

TPH	C		N		C/N	
	absent	present	absent	present	absent	present
no. ha ⁻¹	<u>Mg ha⁻¹</u>		<u>kg ha⁻¹</u>			
154	7.9	10.6	119	158	67.1	68.4
309	8.0	10.4	118	189	68.3	56.6
617	13.6	11.9	255	229	53.5	50.9
1235	8.2	10.8	113	199	72.7	54.8
2469	10.7	18.0	199	406	54.5	44.6
avg.	9.7	12.3	161	236	63.2	55.1
<u>Analysis of variance, $P > F$</u>						
V		0.0115		0.0016		0.0001
TPH		0.0058		0.0002		0.0006
V x TPH		0.1019		0.0277		0.0512
CV. %		23.8		28.5		9.3

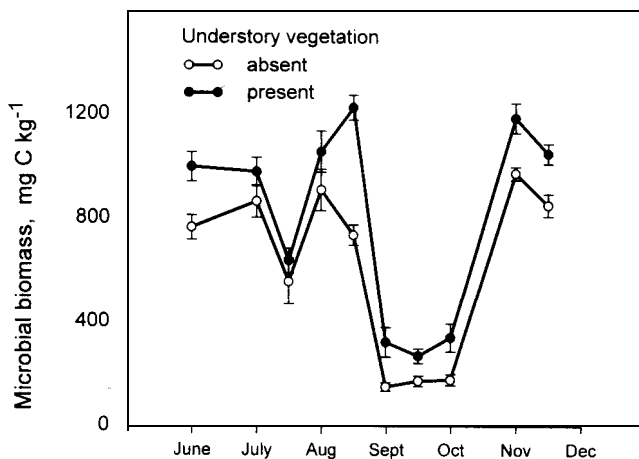


Fig. 3. Seasonal microbial biomass carbon (MBC) at the 0- to 2-cm depth in 1991.

understory vegetation in maintaining or enhancing C levels in ponderosa pine forests. These findings are supportive of long-term studies in agricultural and grassland systems, which have identified changes in total organic C in response to management practices such as tillage and organic supplements (Campbell and Souster, 1982; Lal et al., 1994; Rasmussen and Parton, 1994).

Implied reasons for the 25% greater C content in the upper mineral soil when understory vegetation was present include (i) C input from litter and roots, or (ii) stabilization of organic matter (humus formation). Litter C content, measured in 1994, was 21% greater when understory vegetation was present, suggesting the role of soil mixing or leaching of dissolved organic C from the O horizon. Extensive rooting of shrubs and herbaceous plants would also be expected to contribute additional C; root turnover is considered a major source of C in forested soils (Tate et al., 1993). Stabilization of organic matter was suggested by Johnson (1995) to explain greater soil C concentration under stands of ceanothus compared with adjacent stands of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf). Whether the presence of understory vegetation in our study led to greater stabilization of the humus fraction, and, consequently, less C mineralization cannot be confirmed without further fractionation of soil C.

Thirty-five years of understory vegetation removal also resulted in 212 kg ha⁻¹ less N in the combined O horizon and upper 24 cm of mineral soil in comparison with treatments retaining understory vegetation. Although snowbrush and bitterbrush were found on all plots with understory vegetation present, their low biomass values suggest that N₂ fixation did not contribute substantially to N differences. Aboveground biomass averaged 558 kg ha⁻¹ for snowbrush and 740 kg ha⁻¹ for bitterbrush. Studies of N₂ fixation by snowbrush have found that stands with aboveground biomass ranging from 34000 to 48000 kg ha⁻¹ are capable of fixing between 71 and 101 kg N ha⁻¹ yr⁻¹ (Youngberg and Wollum, 1976; McNabb and Cromack, 1983). Assuming a constant relationship between above-ground biomass and rate of N₂ fixation, snowbrush would be contributing

between 1.0 and 1.2 kg N ha⁻¹ yr⁻¹ at the Pringle Falls site. The amount of N provided by bitterbrush is expected to be even lower. A ¹⁵N-isotope dilution study in central Oregon found only 45 to 70% of bitterbrush N is derived from the fixation of atmospheric N (Busse, 1990, unpublished data). Given the minor role of N₂ fixation at Pringle Falls, we speculate that the observed N accretion in the presence of understory vegetation resulted from increased production and turnover of both roots and/or litter.

Microbial biomass C correlates well with mineralizable N in central Oregon pumice soil (Myrold, 1987) and provides a rapid indication of management effects on soil properties (Sparling, 1992; Bosatta and Agren, 1994). We found greater MBC in soil with understory vegetation present: seasonal MBC averaged 808 mg C kg⁻¹ for treatments with understory vegetation and 614 mg C kg⁻¹ for treatments with understory vegetation absent. These values are higher than previously reported in central Oregon forest soils (Myrold, 1987; Busse, 1994), possibly due to differences in sampling depths between studies.

The long-term changes in soil quality at Pringle Falls are of interest in the context of fire management in ponderosa pine ecosystems. Prescribed underburns were previously thought to increase stand growth by reducing competition from understory vegetation and increasing the availability of nutrients stored in the aboveground organic matter. Evidence now suggests that ponderosa pine sites increase in productivity in the absence of fire (Cochran and Hopkins, 1991). Landsberg (1993) has also shown that underburning reduces the growth of surviving ponderosa pine trees in central Oregon. Modification of soil quality requires consideration, therefore, along with fire danger, wildlife cover and browse, and aesthetics in the management of understory vegetation.

We found the presence of understory vegetation adversely affected the growth of ponderosa pine for about 20 yr only, a short time when compared with a stand rotation of 120 yr or more. Further, presence of understory vegetation resulted in greater soil C, N, and MBC, accepted indices of soil quality (Doran and Parkin, 1994). A long-term benefit to the upper soil horizon is associated with maintaining understory vegetation.

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