SOIL PROPERTIES ASSOCIATED WITH VEGETATION PATCHES IN A *PINUS PONDEROSA*–BUNCHGRASS MOSAIC

Becky K. Kerns[1,2], Margaret M. Moore[1], Michael E. Timpson[3], and Stephen C. Hart[1]

ABSTRACT.—Since Euro-American settlement, fire exclusion and other factors have dramatically altered interior western coniferous forests. Once open and parklike, present-day structure in many southwestern *Pinus ponderosa* forests consists of dense stands of young, small-diameter trees, with small patches of larger, old trees, and relict open bunchgrass areas. Our objectives were to assess differences in soil properties associated with these different vegetation patches. We examined soil morphological characteristics, pH, organic C concentration, total N concentration, C:N ratio, and phytolith concentration from profiles within 6 transects (18 soil pedons) crossing patches of dense stands of small-diameter trees, patchs of old-growth trees, and open grassy areas. Results indicate that old-growth plots had significantly lower A horizon pH and thicker O horizons than grass plots. In general, we found vegetation patches had statistically similar C and N concentrations and C:N ratios for A and B horizons; however, C in the A horizon was positively correlated with O horizon accumulation ($r^2 = 0.79$). Greater accumulation of organic C in the A horizon of forested areas contrasts with commonly reported results from mesic, mid-continental prairie-forest ecosystems but is typical for many arid, semiarid, and humid savanna ecosystems. Phytolith concentration was similar among old-growth pine, dense younger pine, and open grassy plots; the lack of a spatial pattern in phytolith distribution could indicate that grass cover was more spatially continuous in the past. Additionally, this interpretation is consistent with current theories regarding historical vegetation change in these forests.

Key words: forest soils, grassland soils, phytoliths, biosequence, nonmetric multidimensional scaling.

Woody plant abundance has increased substantially during the past several hundred years in many of the world's grasslands and savannas (van Vegten 1983, Arno and Gruell 1986, Archer et al. 1988, McPherson et al. 1993). These increases have been attributed to changes in climate, disturbance, and atmospheric CO_2 concentrations. Prior to Euro-American settlement in the interior western USA, frequent fires maintained open, parklike conditions in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests (Cooper 1960, Dieterich 1980, Covington and Moore 1994a, 1994b, Swetnam and Baisan 1996, Covington et al. 1997, Fulé et al. 1997). Fire suppression, overgrazing, and a warm, wet climatic period led to an irruption of pine regeneration in the early part of the 20th century (Cooper 1960, White 1985, Savage et al. 1996, Mast et al. 1999). Present-day community structure in many southwestern ponderosa pine forests is characterized by a mosaic of dense stands of these small-diameter trees, with small patches of larger, old trees, and relict open bunchgrass areas.

Some 60 years ago, Hans Jenny (1941) outlined the importance of 5 factors that control soil genesis: climate, organisms, topography, parent material, and time. Numerous researchers have examined adjacent forested, recently forested, and grassland areas to determine the biotic factors. In mid-continental prairie and forest ecosystems, coniferous and deciduous forest soils when compared with grassland soils can have, among other factors, thinner A horizons, lower pH values, higher carbon:nitrogen (C:N) ratios, and lower mineral soil organic matter (C and N) accumulation, which decreases more rapidly with depth (White and Riecken 1955, Bailey et al. 1964, Geis et al. 1970, Severson and Arneman 1973, Ugolini and Schlichte 1973, Birkeland 1984, Anderson 1987, Zhang et al. 1988, Almendinger 1990, Fuller and Anderson 1993). This commonly reported pattern in soil properties has also been used to infer past vegetation change and ecotone boundary

[1]School of Forestry, College of Ecosystem Science and Management, Northern Arizona University, and Merriam Powell Center for Environmental Research, Flagstaff, AZ 86011-5018.
[2]Present address: Pacific Northwest Research Station, USDA Forest Service, Corvallis, OR 97331.
[3]Natural Resource Group, Inc., 1000 IDS Center, 80 South Eighth St., Minneapolis, MN 55402.

stability (Birkeland 1984, Zhang et al. 1988, Almendinger 1990, Fuller and Anderson 1993). Differences in soil properties are attributed to grasses being relatively higher quality substrates for soil microflora (low C:N and lignin: N ratio, higher pH) and depositing more organic matter at depth via their root systems compared with deciduous and especially coniferous trees (Meentemeyer 1978, Anderson 1987, Hart et al. 1992, Schimel et al. 1994). Almendinger (1990) concluded that the magnitude of these differences, particularly for soil organic matter and total N, increases the longer the vegetation persists.

Forest soils also have lower phytolith concentration by mass than grassland soils. Phytoliths are particles of hydrated silica formed in the cells of living plants and are liberated upon decomposition. Because of the high silica concentration of grasses compared with coniferous and deciduous trees, soils beneath persistent grassland vegetation typically contain significantly more phytoliths by mass than soils beneath forest vegetation (Jones and Beavers 1964, Witty and Knox 1964, Wilding and Drees 1971, Norgen 1973). Differences in soil phytolith concentration have been used to decipher changes in grassland and forest ecotones through time (Miles and Singleton 1975, Fisher et al. 1987).

Our objectives were to assess differences in soil properties associated with contrasting vegetation patches (sensu White and Pickett 1985) in a ponderosa pine–grassland mosaic. We examined soil morphological characteristics, pH, organic C concentration, total N concentration, C:N ratio, and phytolith concentration along 6 transects (18 soil pedons) from clumps of old-growth trees, dense stands of younger pine trees, and open grassy areas. We hypothesized that (1) open grassy areas would have soil properties typically associated with grasslands, (2) patches of old-growth trees would have soil properties associated with forests, and (3) dense younger pine areas would have soil properties transitional between these 2 areas.

STUDY SITE

The approximately 2-km^2 study site is located in northern Arizona, USA, within the Fort Valley Experimental Forest, about 10 km northwest of Flagstaff. This area has never been logged and is presently excluded from livestock grazing, although cattle and sheep grazing did occur between 1876 and 1910 (Covington et al. 1997). Mean annual precipitation is 56.7 cm, with approximately half falling as snow in the winter and the other half as monsoonal rains from July through September (Schubert 1974). This area has a mean annual air temperature of 7.5°C and an average of 94 frost-free growing days. The topography is fairly level (0%–5% slopes), and mean elevation is 2250 m. Soils are mapped as a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs that developed on Tertiary basalt flows and cinders (Miller et al. 1995).

Ponderosa pine is the only overstory tree within the study area. Understory vegetation consists of bunchgrasses such as *Elymus elymoides* (Raf.) Swezey, *Muhlenbergia montana* (Nutt.) A.S. Hitchc., and *Poa fendleriana* (Steud.) Vasey, and a variety of forbs (Kerns et al. 2001). The only common shrub is *Ceanothus fendleri* Gray.

METHODS

Six transects were chosen randomly from a set of 20 intentionally selected to cross different patches of vegetation. Along each transect we established three 41-m^2 (0.01-acre) circular plots for a total of 18 plots. Transects ranged from 17 m to 26 m in length. Four transects had the following 3 plot types: old-growth pine, transition, and dense younger pine (hereafter, old-growth/young transects). The other 2 transects had the following 3 plot types: old-growth, transition, and grass (hereafter, old-growth/grass transects). We located plots on relatively level terrain within the same soil complex (Miller et al. 1995), on deep soils away from rocky outcrops. Our goal was to establish a biosequence with aboveground vegetation being the only variable that changed (Jenny 1980a). We chose our plot size to be slightly smaller than the smallest patches of vegetation (Kenkel et al. 1989), which were grassy areas. All old-growth plots were established in the center of the tree patch, and all transition plots were located just beyond the canopy dripline of old-growth trees. Grass plots were established within the nearby open grassy area, and dense younger pine plots were entirely within the stand of trees. Only 2 old-growth/grass transects were included in

the study due to the present-day paucity of open grassy areas that were also accessible in the study area by heavy equipment used for soil excavation.

Field Sampling and Laboratory Methods

For each plot we recorded tree density and measured diameter at breast height (1.4 m) of each tree. Trees less than breast height were not counted. To determine age, we cored trees at stump height (40 cm). All trees within the old-growth plots were cored, and a random 10% sample of trees was cored in the dense younger pine plots. Using cover classes (Daubenmire 1959), we estimated understory plant canopy cover (shrub, forb, grass). Remaining cover on the plot was assigned to other ground cover classes (e.g., forest floor). Soil pits were then mechanically excavated within the center of each plot using a truck-mounted backhoe, described (texture by feel, color, structure, etc.), and then sampled by genetic horizon (Soil Survey Staff 1993).

We collected phytolith samples prior to soil excavation because backhoe use was restricted during most of the summer due to severe fire danger. This initial sampling allowed us to proceed with laborious phytolith extraction procedures. At the plot center we systematically removed 10 mineral soil cores, separated them into 2 depth intervals (0–2 cm and 2–7 cm), and composited them by interval. The 0–2 cm interval was chosen to represent the modern soil surface, which should reflect contemporary grass-tree vegetation patterns (Pearsall 1986, Piperno 1988). The 2–7 cm subsurface interval was selected because we wanted to sample systematically only within the A horizon, which can be as shallow as 7 cm in some places in the study area. Phytoliths are rarely found in other genetic horizons.

Tree cores were mounted and sanded, and rings were counted using standard techniques (Stokes and Smiley 1996). Soils were air-dried before being ground with a wooden rolling pin to pass through a 2-mm sieve, and a subsample was oven-dried at 105°C. Soil texture was determined using the hydrometer method to measure clay content (Gee and Bauder 1986) and wet sieving to determine sand fraction. We determined silt contents by difference and soil pH values using a 2:1 (v:m) suspension of 0.01 M $CaCl_2$:soil (Henderson et al. 1993).

Samples analyzed for C and N concentrations were finely ground using a ceramic mortar and pestle. We titrimetrically measured carbon concentration using a wet oxidation-diffusion method (Snyder and Trofymow 1984), which uses heat (120°C) to oxidize organic matter more completely than traditional wet oxidation methods do. Soils did not react to dilute hydrochloric acid, and all pH values were <7, accounting for our reporting C as organic C. Total N was determined by Kjeldahl digestion and subsequent analysis of the digestate on a Lachat AE Flow Injection Autoanalyzer using the salicylate method (Lachat Instruments 1992).

Using a modified heavy liquid flotation technique (Kerns et al. 2001), we determined soil phytolith concentration gravimetrically. All elemental and phytolith concentrations are expressed relative to the oven-dry mass of soil.

Data Analyses

Data were analyzed within each transect type using a single-factor ANOVA, with plot type (i.e., old-growth, grass, dense young pine) as the independent factor. If statistically significant ($\alpha = 0.10$), differences were compared using Tukey's correction procedure for multiple comparisons ($\alpha = 0.10$). We chose this alpha level *a priori* due to our low sampling intensity necessitated by the laborious nature of soil profile descriptions. Relationships between variables (C and N concentrations, C concentration and O horizon thickness) were explored using least-squares regression. Because soil horizons were generally broken into several units for sampling purposes in the field, we calculated mean values for whole horizons using a weighted mean based on subsample depth. Mean values are reported along with 1 standard error of the mean ($\pm s_{\bar{x}}$). All statistical analyses (except ANOSIM and the ordination described below) were completed using SYSTAT 8.0 (SPSS Inc. 1998).

To examine the degree of similarity between vegetation and soil properties considering all variables together, we used 2 multivariate techniques: ANOSIM, a multivariate analysis of variance to test for statistically significant differences (using a distribution-free random-permutation procedure), and NMDS (nonmetric multidimensional scaling), a robust ordination technique (Kruskall 1964, Minchin 1987). Ordinations are useful in showing spatial structure

TABLE 1. Vegetation characteristics grouped by plot type from old-growth/grass (A) and old-growth/dense younger pine transects (B). Overstory data are means ($\pm s_{\bar{x}}$). Understory cover data are means ($\pm s_{\bar{x}}$) calculated using midpoint cover classes. Values from the same row with different lowercase letters are statistically significantly different ($P < 0.10$).

Transect set A	Old-growth	Transition	Grass[1]
Live overstory trees			
Density (trees per plot)	3.0 (0.0)a	0.5 (0.5)b	0.5 (0.5)b
Dbh (cm)	64.8 (3.5)a	14.5 (0.0)b	28.5 (0.0)b
Number of rings	229.6 (27.7)a	56.0 (0.0)b	64.0 (0.0)b
Understory cover (%)[2]			
Grass	8.7 (6.2)a	25.0 (0.0)ab	50.5 (12.5)b
Forb	2.5 (0.0)a	2.5 (0.0)a	7.5 (7.5)a
Shrub	0.0 (0.0)a	0.2 (0.2)a	1.2 (1.2)a
Forest floor cover (%)	91.2 (6.2)a	21.2 (16.2)b	8.8 (6.2)b

Transect set B	Old-growth	Transition	Dense younger pine
Live overstory trees			
Density (trees per plot)	4.0 (0.6)a	27.8 (9.0)b	33.5 (6.3)b
Dbh (cm)	65.1 (4.7)a	6.8 (0.4)b	7.9 (0.4)b
Number of rings	249.1 (17.9)a	55.9 (1.5)b	60.7 (1.6)b
Understory cover (%)[2]			
Grass	5.6 (3.1)a	23.8 (13.2)a	14.8 (8.2)a
Forb	2.5 (0.0)a	2.5 (0.0)a	2.5 (0.0)a
Shrub	0.0 (0.0)a	0.8 (0.6)a	0.6 (0.6)a
Forest floor cover (%)	73.8 (6.5)a	58.8 (19.5)a	73.8 (6.5)a

[1]Grass plot from transect 1 included 1 small young tree.

[2]Zero standard errors and identical values are due to the use of midpoint cover class values.

of multivariate data and similarity and dissimilarity of samples, based on all variables of interest considered together. The most important property of an NMDS ordination is the pattern of relative distances among pairs of points; ordination axes are arbitrary and have no significant meaning. Examination of plots of stress, a normalized measure of badness of fit, versus the number of dimensions (1–4) provides a guide to the minimum number of dimensions required to adequately describe the data (Kruskall 1964). For ordinations presented in this paper, 2 axes appeared to adequately represent the data sets. Both ANOSIM and NMDS were performed using the program DECODA Version 3.0 (software available from ANUTECH Pty. Ltd., at www.anutech.com.au/TD/DECODA_WWW/welcome.html).

RESULTS

Vegetation

Statistical analyses of vegetation confirmed our plot selection criteria (Table 1). For the old-growth/grass transects, old-growth plots had a significantly smaller percentage of grass cover and more forest floor cover than grass plots but no difference in forb or shrub cover was found. For the old-growth/dense younger pine transects, no difference in grass, forb, shrub or forest floor cover was found. Dense younger pine plots had significantly denser stands of younger, smaller trees than old-growth plots. Mean number of rings for younger pine trees (60.7 ± 1.6) plus 3–10 years to reach coring height (40 cm) indicates a germination date between 1925 and 1932. Cores were not cross-dated to check for missing rings, and it is likely that some of these trees are from the extensive 1919 cohort documented in the study area (Savage et al. 1996, Mast et al. 1999).

Soil Properties

For the old-growth/grass transects, we detected a significant difference for O horizon thickness, an evident conclusion since only the old-growth plots had a measurable O horizon (Table 2). No difference was detected for A horizon thickness. Soil texture of the A horizon for all 18 plots was silt loam. A horizon pH values were significantly lower for old-growth plots than for both transition and grass plots. For the old-growth/young pine transects, old-growth plots had significantly thicker O horizons

TABLE 2. Soil properties and classification grouped by plot type from old-growth/grass (A) and old-growth/dense younger pine transects (B). Data are means (± $s_{\overline{x}}$). Values from the same row with different lowercase letters are statistically significantly different ($P < 0.10$).

Transect set A	Old-growth	Transition	Grass
O horizon thickness (cm)	11.0 (2.0)a	0.0 (0.0)b	0.0 (0.0)b
A horizon thickness (cm)	11.2 (3.7)a	16.5 (5.5)a	22.5 (5.5)a
pH (0.01 M CaCl$_2$)	5.4 (0.10)a	5.8 (0.20)b	6.0 (0.05)b
Phytolith concentration (%)			
Depth (cm)			
0–2	2.5 (0.78)a[1]	2.0 (1.10)a	1.5 (0.52)a
2–7	1.5 (0.06)a	2.1 (0.95)a	1.6 (0.02)a

Transect set B	Old-growth	Transition	Dense younger pine
O horizon thickness (cm)	9.0 (2.1)a	3.2 (0.6)b	3.2 (0.9)b
A horizon thickness (cm)	17.0 (1.4)a	19.2 (3.7)a	18.8 (1.6)a
pH (0.01 M CaCl$_2$)	5.6 (0.10)a	5.8 (0.04)a	5.7 (0.05)a
Phytolith concentration (%)			
Depth (cm)			
0–2	1.9 (0.22)a	1.0 (0.41)a	1.9 (0.45)a
2–7	1.9 (0.19)a	1.5 (0.24)a	1.8 (0.27)a

[1]For phytolith concentration, lowercase letters also represent statistical results within the same column (depth; $P < 0.10$).

compared with transition and dense younger pine plots, but no differences in A horizon thickness or pH were detected.

For both sets of transects, we found few significant differences among plots for A and B horizons, C concentration, N concentration, and C:N ratio (Fig. 1). Examination of individual transects indicates that C and N concentrations were generally lower throughout the profile for grass plots than old-growth plots (Appendix). The extent of this difference was much greater for C. The grass plot from transect 18 showed an increase in C concentration with depth in the A horizon, suggesting that deposition of new material on an older surface (lithological discontinuity) could have occurred at this location. Examination of individual transects also shows that old-growth plots had generally higher C and N concentrations in the A horizon compared to dense younger pine plots, but C and N were very similar within B horizons (Appendix).

Not surprisingly, analysis of C and N concentrations from all plots demonstrated a high correlation between N and C ($n = 79$, $r^2 = 0.94$, $P < 0.01$). Carbon concentration in the A horizon was positively correlated with O horizon thickness (Fig. 2; $n = 16$, $r^2 = 0.79$, $P < 0.001$). Two samples were statistically tested as outliers (Studentized Deleted Residual Procedure, Neter et al. 1990) and discarded.

No differences in mass recovery of phytolith material based on plot type were detected for either depth (Table 2). Likewise, phytolith mass was similar in the surface (0–2 cm) and subsurface (2–7 cm) depths.

Ordination results show plot types distinctly clustered based on soil properties (A horizon thickness, O horizon thickness, pH in the A horizon, and C:N in the A and B horizons; Fig. 3a), and these distinct differences among plot types were significant (ANOSIM, $P = 0.001$, $n = 18$). Note that dense younger pine plots were grouped between grass and old-growth plots. Because differences in O horizon accumulation were so dramatic, we reanalyzed the data without this variable. Removal of this variable resulted in no significant difference being detected, and the new ordination showed that plot types were not as distinctly grouped (Fig. 3b). However, some degree of separation was apparent, particularly for old-growth and grass plots.

DISCUSSION

Frequently, detailed analyses and other factors limit extensive sampling and inference in pedogenic studies; however, several interesting results emerged in our study. The major difference in soil properties that we detected among our plots was that old-growth plots had
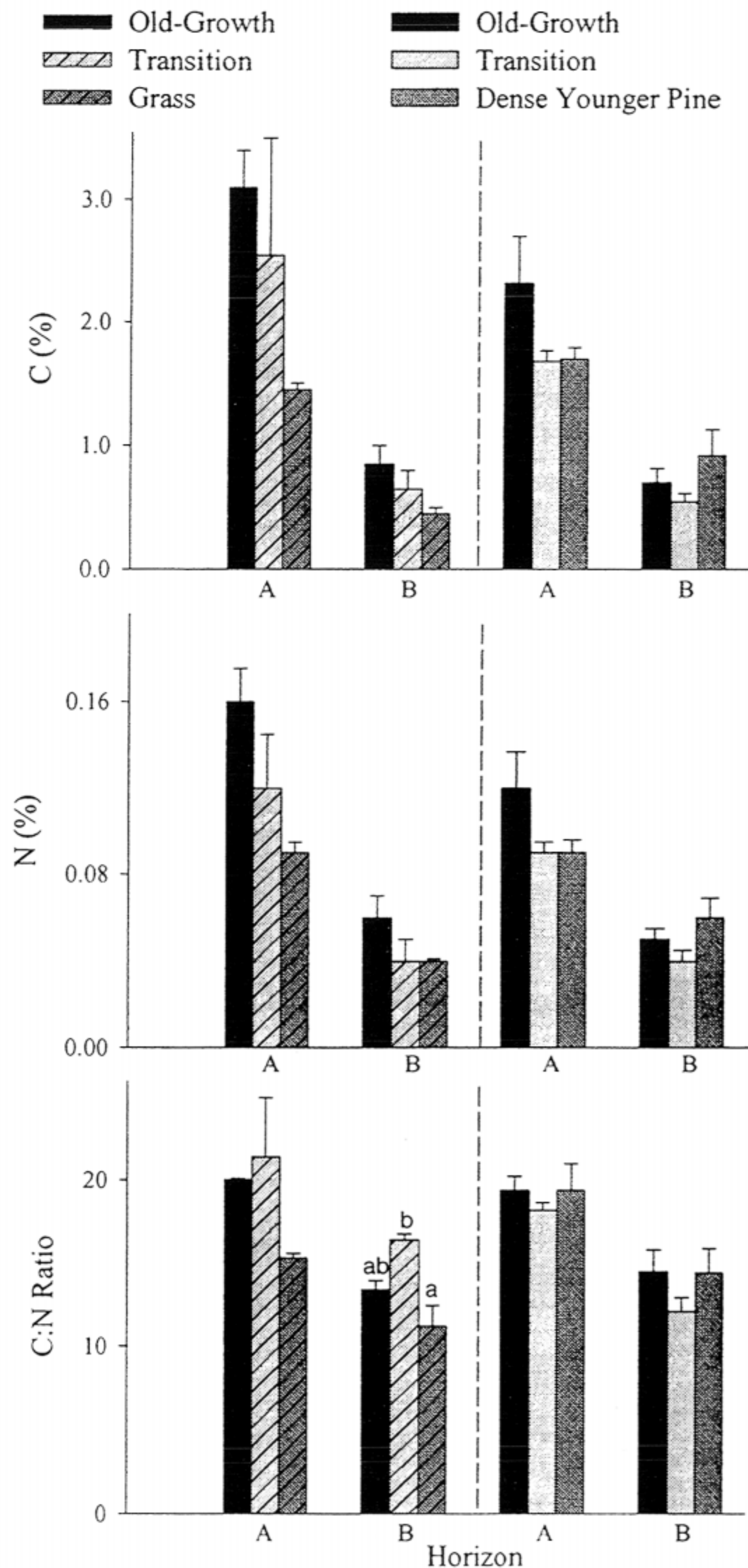
Fig. 2. Organic C concentration in the A horizon as a function of O horizon thickness ($r^2 = 0.79$, $n = 16$, $P < 0.001$). Two plots were tested as outliers (Studentized Deleted Residual Procedure) and are not included in model statistics but are shown in the figure.

Fig. 1. Soil organic C concentration, total N concentration and C:N ratios for A and B horizons grouped by plot and transect type. Data are means ($\pm s_{\bar{x}}$).

mid-continent (White and Riecken 1955, Bailey et al. 1964, Geis et al. 1970, Severson and Arneman 1973, Almendinger 1990, Fuller and Anderson 1993). However, this pattern has been found in ponderosa pine forests (Potter and Green 1964, Jenny 1980a) and is commonly reported in arid, semiarid, and humid savanna ecosystems (Jackson et al. 1990, Weltzin and Coughenour 1990, Isichei and Muoghalu 1992, Vetaas 1992, Mordelet et al. 1993, Hibbard 1995, McPherson 1997) and pinyon and juniper ecosystems (Klopatek 1986, Tiedemann 1986).

Factors such as litter quality, microsite conditions, and relatively low grass productivity could explain higher C and N accumulation in forested areas in arid and semiarid forest ecosystems. In our study area grassland productivity (11.2 g · m^{-2} · y^{-1} for grassy areas; Covington et al. 1997) is much lower than the mesic mid-continental prairie, where tallgrass and mixed-grass prairie ecosystems typically produce 100–300 g · m^{-2} · y^{-1} (Barbour et al. 1999). In addition, O horizons were composed predominantly of ponderosa pine needles, bark, and woody material that had accumulated beneath trees on forested plots. Ponderosa pine litter is characterized by high C:N and lignin:N ratios, which, in part, are responsible for low decomposition rates of this litter type (Welch and Klemmedson 1975, Klemmedson et al. 1985, Hart et al. 1992). Lack of a significant O

significantly lower A horizon pH values and thicker O horizons than either grass or dense younger pine plots. Our pH results were as predicted, but in contrast to our hypothesis, we found that soils from different vegetation patches generally had similar C and N concentrations and C:N ratios. However, C in the A horizon was positively correlated with O horizon thickness. Greater accumulation of organic C in the A horizon of forested areas contrasts with results reported for the mesic
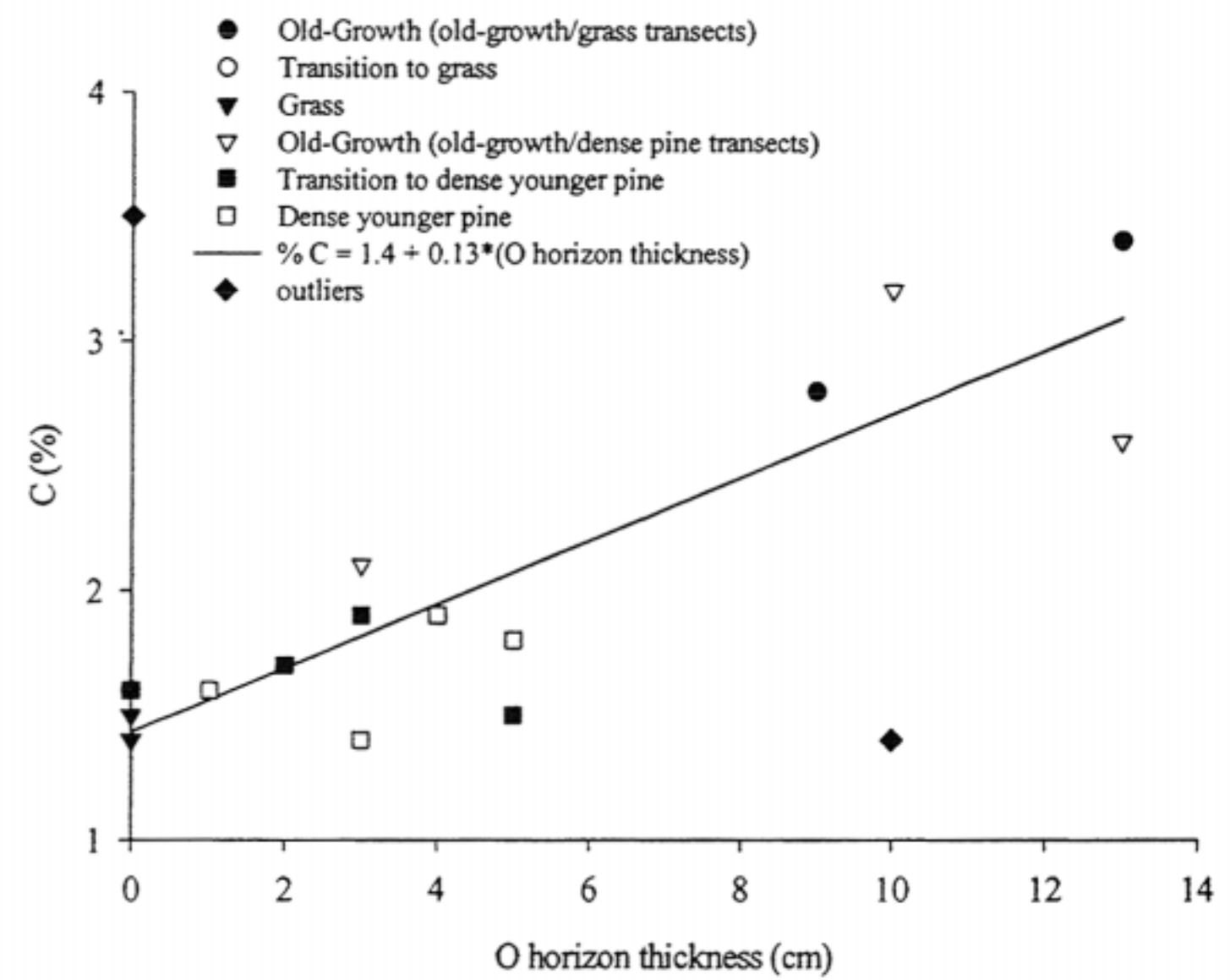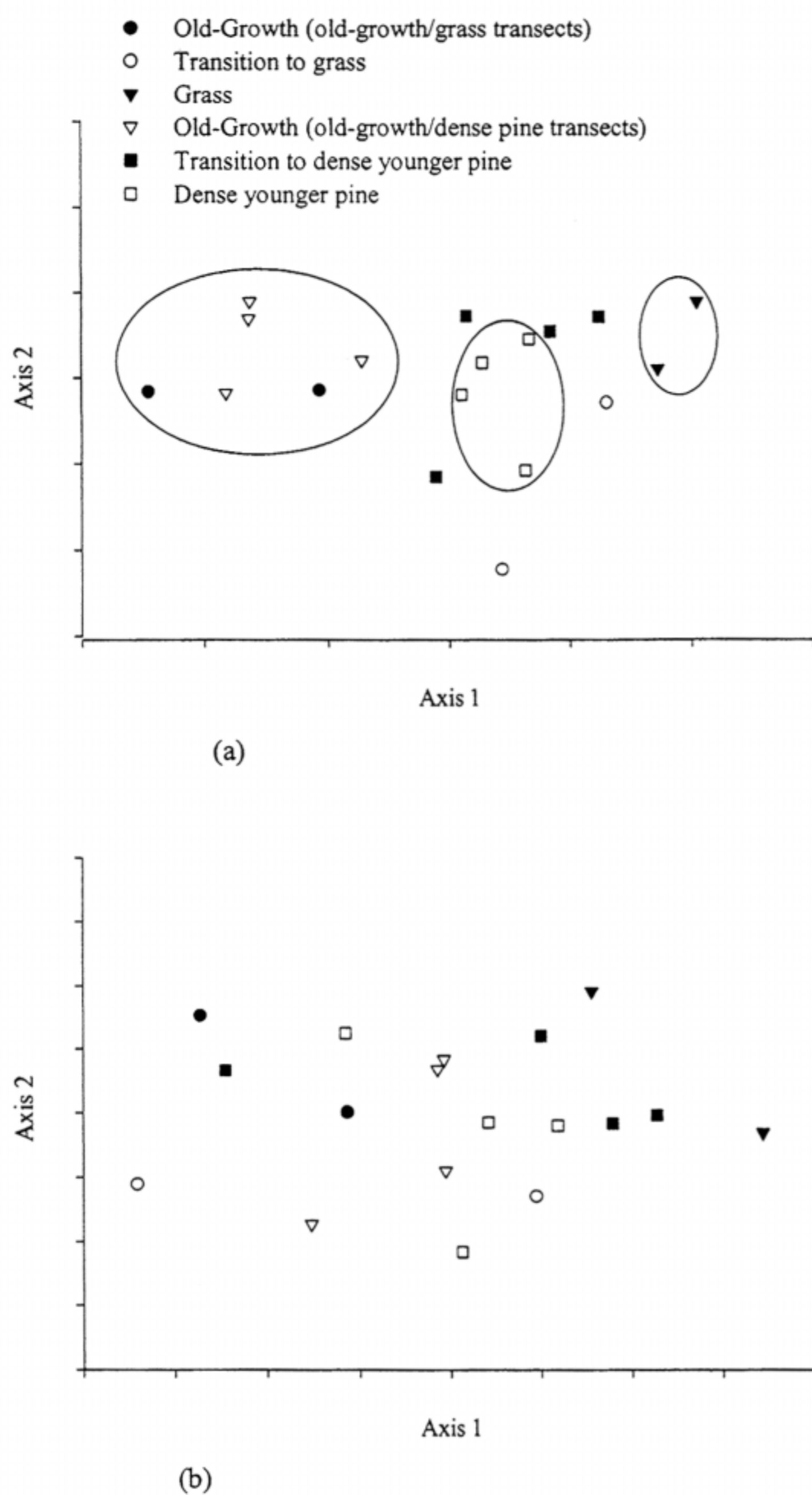
(a)

(b)

Fig. 3. (a) Ordination scores from an NMDS analysis show distinct groupings for vegetation types based on 5 soil characteristics (ANOSIM, $n = 18$, $P = 0.001$). Old-growth, grass, and dense younger pine plots are circled for clarification. (b) Ordination scores from a repeated NMDS analysis with the O horizon thickness variable removed show much less distinct groupings, suggesting O horizon thickness was the variable responsible for most of the grouping shown in (a) (ANOSIM, $P > 0.10$). Axes and scales are not directly comparable between the 2 ordinations.

horizon and low soil C and N beneath grass plots could be a result of more rapid decomposition rates in these areas. Low levels of nutrient accumulation can be characteristic of rapid cycling rates, especially for more arid ecosystems (Schlesinger et al. 1990). In an area adjacent to our study area, Kaye and Hart (1998a, 1998b) showed that mineral soil net N mineralization, nitrification, and respiration were significantly higher in patches of grass compared to dense younger pine stands and

old-growth tree stands. Open areas also have higher solar radiation, soil temperature, and soil moisture during the growing season than dense pine-dominated areas (Covington et al. 1997). Therefore, low soil C and N accumulation beneath our grass plots could be the result of more rapid cycling rates of material in these areas.

Interestingly, phytolith concentration was similar between plots for both the 0–2 cm and 2–7 cm intervals. The 0–2 cm interval probably reflects the past 100–200 years (Fredlund and Tieszen 1994), and the 2–7 cm depth an older association. Our results do not demonstrate the dramatic differences in phytolith concentration previously reported from forest and grasslands soils (Jones and Beavers 1964, Witty and Knox 1964, Wilding and Drees 1971, Norgen 1973, Miles and Singleton 1975, Fisher et al. 1987) and could indicate that grass cover was more spatially continuous in the past. This interpretation is consistent with studies based on fire history, historical photos, dendrochronology, and inference from population structure (Cooper 1960, Covington and Moore 1994a, 1994b, Covington et al. 1997, Fulé et al. 1997), all of which suggest that historical expansion of ponderosa pine has occurred at the expense of open grassy areas.

In conclusion, the major differences in soil properties that we detected were significantly lower A horizon pH values and thicker O horizons for old-growth plots than for grass and dense younger pine plots. Lack of other statistically significant results could be due to our low sample size, inherent variability in soils, and difficulty of truly isolating the tightly coupled factors of soil genesis. For example, it is possible that potential effects of parent material and soil texture have obscured organic matter patterns derived from vegetation. Fine-textured, smectitic soils derived from basalt parent materials have a high capacity to accumulate and retain organic matter (Welch and Klemmedson 1973, Jenny 1980b, Nichols 1984). In an ecosystem with coarser-textured soils, differences in soil properties due to vegetation may be more pronounced. This could also explain why marked differences in soil properties were found in many classic forest-prairie transition studies conducted in areas with recent glacial parent materials. Yet, Welch and Klemmedson (1975) reported greater C and N concentrations in soils from grass openings compared to

young pole-sized ponderosa stands on similar fine-textured (silt loam) basalt soils in northern Arizona. It is also possible that the temporal stability of vegetation patches in our study area is insufficient to create a significant biotic signature.

ACKNOWLEDGMENTS

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See appendix on the following page.

APPENDIX. Individual sample values for mineral soil organic C concentration and total N concentration (%) and C:N ratios by depth for horizons and subsamples grouped by plot type from old-growth/grass and old-growth/dense younger pine transects.

Transect	Old-growth				Transition				Grass			
Horizon	Depth[a]	C%	N%	C:N	Depth	C%	N%	C:N	Depth	C%	N%	C:N
1												
A	0–7.5	3.4	0.17	20.0	0–11	3.5	0.14	25.0				
A1									0–7	1.7	0.09	18.9
A2									7–17	1.2	0.08	15.0
BA	7.5–15	1.3	0.09	14.4								
Bt1	15–40[b]	1.0	0.07	14.3	11–48	0.7	0.05	14.0	17–39	0.8	0.07	11.4
Bt2	40–65[b]	0.8	0.05	16.0	48–95	0.3	0.02	15.0	39–67	0.2	0.02	10.0
Bt3									67–103	0.3	0.03	10.0
18												
A									0–9[b]	1.0	0.07	14.3
A1	0–7	3.7	0.17	21.8	0–5	3.0	0.15	20.0				
A2	7–15	2.1	0.11	19.1	5–22	1.2	0.08	15.0	9–18[b]	1.4	0.09	15.6
2A1									18–28[c]	2.1	.013	16.2
Bt									28–49	0.7	0.05	14.0
Bt1	15–40[b]	1.1	0.07	15.7	22–40[b]	0.9	0.05	18.0				
Bt2	40–60[b]	1.0	0.06	16.7	40–60[b]	0.7	0.04	17.5				
BCt	60–73	0.9	0.05	18.0								
BCt1									49–70[b]	0.5	0.04	12.5
BCt2									70–94[b]	0.5	0.04	12.5
Cbt/Cr	73–110+	0.3	0.03	10.0								

Transect	Old-growth				Transition				Dense younger pine			
Horizon	Depth	C%	N%	C:N	Depth	C%	N%	C:N	Depth	C%	N%	C:N
11												
A	0–15	2.6	0.14	18.6								
A1					0–10	2.1	0.11	19.1				
1A1									0–7	2.5	0.12	20.8
A2					10–24	1.2	0.08	15.0				
2A2									7–21[c]	1.7	0.08	21.3
3Bt									21–68	0.9	0.07	12.9
Bt1	15–43[b]	1.1	0.06	18.3	24–50	0.5	0.06	8.3				
Bt2	43–67[b]	0.7	0.05	14.0	50–82	0.4	0.03	13.3				
12												
A					0–9	1.9	0.10	19.0				
A1	0–5[b]	1.5	0.09	16.7					0–7[b]	1.7	0.07	24.3
A2	5–10[b]	1.3	0.09	14.4					7–14[b]	1.4	0.07	20.0
A3	10–15	1.3	0.08	16.3								
Bt1	15–38	0.7	0.06	11.7	9–22	1.5	0.08	18.8	14–31	0.9	0.06	15.0
Bt2	38–56	0.5	0.05	10.0	22–58	0.5	0.04	12.5	31–62	0.5	0.04	12.5
Bt3	56–88	0.5	0.03	16.7	58–82	0.5	0.04	12.5	62–82	0.4	0.03	13.3
16												
A	0–17	2.0	0.10	20.0					0–20	1.8	0.10	18.0
A1					0–9	1.9	0.10	19.0				
A2					9–19	1.1	0.08	13.8				
BA									20–39	1.8	0.08	22.5
Bt1	17–37[b]	0.8	0.06	13.3	19–50	0.5	0.05	10.0	39–68	1.0	0.06	16.7
Bt2	37–77[b]	0.5	0.03	16.7	50–100	0.3	0.03	10.0	68–111	0.4	0.03	13.3
Bt3	77–117	0.3	0.03	10.0								
20												
A	0–21	3.2	0.15	21.3								
A1					0–9	2.7	0.15	18.0	0–6	2.0	0.11	18.2
A2					9–25	1.2	0.08	15.0	6–20	1.2	0.07	17.1
Bt									20–68	0.7	0.06	11.7
Bt1	21–44	1.2	0.07	17.1	25–50	0.8	0.06	13.3				
Bt2	44–80	1.0	0.06	16.7	50–100	0.8	0.05	16.0				
BC	80–130	0.6	0.04	15.0	100–120	0.5	0.03	16.7				
BCt									68–104	0.9	0.05	18.0

[a]All depths in cm
[b]Horizon designations (i.e., A1, A2, Bt1, Bt2) were primarily for subsampling and do not necessarily relate to soil genesis.
[c]Lithological discontinuity