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Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest

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Abstract Soil thickness can be an important factor influencing vegetation, yet few spatially-explicit studies have examined soil horizon thickness and vegetation composition in summer-drought forests. We compared seismic and soil penetration measurements of combined A + C and Cr horizon thickness, soil moisture and temperature, and stand variables in a contiguous 4-ha mixed-conifer stand of the Sierra Nevada. Thickness of A + C and Cr horizons were highly variable but were not correlated to each other. Total basal area and canopy cover were positively related with A + C horizon thickness, and shrub cover was positively related with Cr horizon thickness. Basal area of white fir [*Abies concolor* (Gord and Glend) Lindl.] and incense-cedar [*Calocedrus decurrens* (Torrey) Florin] were positively correlated with A + C horizon thickness, but there was no relationship between A + C or Cr horizon thickness and basal area of Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.), sugar pine (*P. lambertiana* Douglas), or red fir (*A. magnifica* A. Murray). Both white and red fir seedlings were associated with decreased soil temperature, but only white fir seedlings were positively associated with soil moisture. Soil penetration estimates of soil thickness were similar to seismic estimates for shallow soils (<50 cm depth) but were poorly related on deeper soils. Visual surface conditions and tile probe estimates of soil thickness can be highly misleading because 'shallow' areas may have a thick layer of weathered bedrock that can serve as a potential rooting medium for deep-rooted trees and shrubs. In our study only the refraction seismic method had the potential to measure total soil depth that included A + C and Cr horizon thickness.

Keywords Forest regeneration · Refraction seismic method · Soil moisture · Soil temperature

Introduction

Soil is the fundamental substrate of forest ecosystems and has a functional role in decomposition,

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nutrient cycling, net primary productivity, water supply, food webs, and stand dynamics (Wall and Moore 1999; Fisher and Binkley 2000). Many factors influence a soil's productivity, including organic and mineral content, porosity, microbial biomass, temperature, and moisture (Fisher and Binkley 2000). In seasonally-dry forest ecosystems, soil thickness can be an important influence on productivity and stand features because it strongly affects potential root volume, plant-available water, hydrologic function, vertical temperature profile, and buffering capacity (Poff 1996). In some forests, soil thickness can limit stand basal area (Fralish 1994), productivity (Romanya and Vallejo 2004), and tree recruitment (Dovčiak et al. 2003), and influence tree species composition across the landscape (Stohlgren and Bachand 1997).

Upper mineral soil layers (including A, B, and C horizons) are important for forest vegetation, with thicker layers often associated with greater root biomass and plant productivity (Jackson et al. 1996). Water-holding capacity and nutrient conditions in these upper horizons may be crucial for tree seedlings and understory shrubs that often have roots concentrated at shallow soil depths (Royce and Barbour 2001; Rose et al. 2002). Recently, more attention has been given to the importance of the lower soil layers (i.e., deep regolith; Zanner and Graham 2004) that includes the parent material important for growth of deep-rooted plant species (Canadell et al. 1996), and soil genesis and respiration (Richter and Markewitz 1995). Deeper soil horizons may be important for plant growth and productivity, especially in warmer moisture-limited forests and woodlands where trees and shrubs exhibit deep rooting profiles that extend into weathered bedrock substrates (i.e., Cr horizon; Arkley 1981; Wang et al. 1995; Sternberg et al. 1996; Hubbert et al. 2001a; Rose et al. 2002; Witty et al. 2003). Few studies, however, have examined the relative importance of these two different soil layers for shrub, tree, and seedling composition and density in a moisture-limited coniferous forest stand.

In California's Sierra Nevada, where seasonally-dry soils are commonly thin (<200 cm) and underlain by Cr horizons of weathered granitic bedrock (Witty et al. 2003), soil thickness is suspected to have a strong influence on soil water availability, and stand composition and density (Urban et al. 2000). In mixed-conifer forests, denser stands of fir (*Abies* spp.), sugar pine (*Pinus lambertiana* Douglas), and incense-cedar [*Calocedrus decurrens* (Torrey) Florin] are often observed on apparently thicker and cooler soil microsites, while lower density stands dominated by shrubs or Jeffrey pine (*P. jeffreyi* Grev. & Balf.) are considered indicative of shallow and exposed mineral soils (Vasek 1978; North et al. 2002). Seedlings of red fir, sugar pine, and incense-cedar also have greater occurrence and survivorship in moister, cooler, less exposed (Barbour et al. 1990; Gray et al. 2005), and deeper (red fir; Barbour et al. 1998) soil microsites. In contrast, shrubs and Jeffrey pines may effectively colonize and grow on shallow mineral soils by developing more extensive root systems (Royce and Barbour 2001) or extracting moisture from weathered bedrock during the hot and dry summer months (Hubbert et al. 2001a, b; Rose et al. 2002; Witty et al. 2003). This deeper moisture may be critical to the recruitment and survival of deep-rooted trees and shrubs in summer-drought forests, because total plant-available water storage in weathered bedrock can exceed twice the amount in soil during the summer (Hubbert et al. 2001b).

Estimation of mineral soil thickness with soil penetration methods (e.g., tile probe) is standard procedure for soil sampling conducted in forest research (e.g., Smallidge and Leopold 1994; Lookingbill and Urban 2004). These methods can provide relatively accurate estimation of soil thickness in the upper 50 cm of soil (e.g., Fuhlendorf and Smeins 1998), especially in the absence of cobbles or broken parent material. In comparison, seismic soil thickness estimation can be a useful tool for determining thickness of mineral soil, weathered bedrock, and total regolith thickness, especially in deeper (>200 cm) soils and at lower soil depths with higher densities of fragmented parent material and homogenous soil moisture profiles (Haeni 1986; Meju et al. 2003). In combination, seismic and soil penetration methods could provide complimentary estimates of soil thickness, but the two methods have not been directly compared in many forest soils.

The objectives of this study were to examine the influences of soil thickness (A + C and Cr horizons) on the density and composition of trees, shrubs, and tree seedlings in a single Sierra Nevada mixed-conifer forest stand. We predicted that total basal area, canopy cover, and occurrence and seedling densities of white fir [*A. concolor* (Gord and Glend) Lindl.], red fir (*A. magnifica* A. Murray), incense-cedar, and sugar pine would be positively related to A + C horizon thickness, while shrub cover and occurrence of Jeffrey pine would be more strongly related to thickness of the Cr horizon. We also predicted seedlings of incense-cedar and sugar pine would be positively associated with moist microsites, and seedlings of white fir and red fir would be positively associated with cool and moist microsites. Additionally, we compared soil thickness measurements made with a tile probe to seismic soil thickness measurements to assess the relationship between these methods above and below 50 cm depth. The expense of seismic methods constrained our sampling to a 4 ha area within the Teakettle Experimental Forest. Within the selected sample area, however, extensive mapped data sets allow us to compare soil depth, moisture, and temperature with vegetation composition.

Materials and methods

Study Site

We conducted our study at the Teakettle Experimental Forest, located in the southern Sierra Nevada of California. Teakettle Experimental Forest (1,800–2,400 m elev., 36°58′N latitude and 119°2′W longitude) experiences hot, dry summers, and precipitation (mean is 125 cm/year at 2,100 m) that falls almost exclusively in the form of snow from November to April (North et al. 2002). Dominant trees include white fir, red fir, sugar pine, Jeffrey pine, and incense-cedar. Dominant shrubs include mountain whitethorn (*Ceanothus cordulatus* Kellogg; 11.0% cover), greenleaf manzanita (*Arctostaphylos patula* Greene, 2.1% cover), California hazelnut (*Corylus cornuta* Marshall *californica* (A. DC.) W.M. Sharp, 2% cover), and bush chinquapin (*Chrysolepis sempervirens* (Kellogg) Hjelmquist, 1.5% cover; based on understory plant surveys in 2002). Teakettle Experimental Forest is an old-growth forest characterized by a multi-layered canopy and numerous large (>100 cm dbh) trees (many >200 years), snags, and decayed logs. There has not been a widespread fire at Teakettle since 1865 (North et al. 2005), and thinning has not occurred within the study area with the exception of 48 ha of forest that was experimentally thinned adjacent to the study site (North et al. 2002). Mean slope of the study site was 9% with a southwest-facing aspect.

Teakettle's most common soils are mixed, frigid Dystric Xeropsamments (Cagwin series), formed from decomposed granite, typical of many soils in the southern Sierra Nevada (Giger and Schmitt 1983). Litter and upper and lower soil layers vary across the study area, and all soils are derived from decomposed granite with similar texture, very low (<5%) clay content, and low water-holding capacity (North et al. 2002). All sample points in this study were on Cagwin soils defined by an A horizon of brown gravelly, loamy coarse sand with weak granular structure and a mean soil pH of 5.4, the absence of a B horizon, a C horizon of soft, very friable mineral soil, and an underlying Cr horizon of weathered bedrock usually encountered below 50 cm depth and overlying hard bedrock (North et al. 2002).

Vegetation measurements

We conducted our study in an intensively sampled 4-ha plot located in one untreated plot of the Teakettle Experiment (18 plots total with six treatments). Plots were sized and located so that they contained a representative composition of patch and forest conditions within mixed-conifer forest (North et al. 2002). Within this 4-ha plot, all trees and snags >5 cm dbh and shrubs (≥4 m^2 in area) were measured in 2002–2003. Trees were measured, and tree and shrubs were identified to species and mapped [position coordinates (*x*, *y*, and *z*)] using a surveyor's total station (Criterion 400 and Topcon 300, LTI, Denver, CO, USA). All coordinates were converted to Universal Transverse Mercator units and elevation using a ground-based corrected global positioning system reading for the initial station location. We established 49 sample points within the 4 ha plot in a seven by seven grid with 25 m spacing between points and a 25-m buffer from the plot boundary. In June through August 2002, understory shrub and herbaceous vegetation cover was measured within a 1.8 m radius (10 m^2) of each sample point, and seedlings (5–50 cm in height) of the five dominant overstory tree species were counted within a 3.5 m radius (38.5 m^2) of each grid point. Using the 4 ha stem map, basal area was estimated for all trees within 12.6 m (0.05 ha) of a sample point and weighted by distance from the plot center. We used weighting to account for the potentially stronger correlation between soil thickness and vegetation rooted directly over the plot center where thickness was measured. In our weighting, the basal area of all trees within 3 m of the plot center was multiplied by 1.0 and all trees >3 m from the center was multiplied by 1.0–0.1 ($\beta - 3$), where β = distance from the plot center.

We expected the abundance and composition of tree seedlings to be highly influenced by soil moisture and temperature (Gray et al. 2005) in addition to the possible influence of soil horizon thickness. Therefore, we measured relative differences in percent soil volumetric water content at 0–15 cm depth between 0800 and 1800 for the same day, 14 August 2002, using time domain reflectometry (TDR), following methods described by Gray and Spies (1995). We did not calibrate soil moisture values to changes in sample time during the day because TDR measures are very robust to changes in soil temperature (Czarnomski et al. 2005), and soil temperature (10 cm depth) was weakly correlated ($r = 0.134$, $P = 0.003$) with time of day during sampling. Soil moisture data collected at 402 sample points for 5 years at Teakettle indicates a consistent pattern in which soils start out at field capacity after snow melt (usually mid-May) and dry down during the summer. We used August measurements because it is at the end of the growing season and typically has the lowest soil moisture readings of the year (A.N. Gray, personal observation). Soil temperature was recorded on 8 August 2002 at all 49 points at 10 cm depth ($T_{10\ \mathrm{cm}}$, °C) using a digital thermometer (Taylor Digital Max/Min, Forestry Suppliers, Inc., Jackson, MS, USA). Measurements were taken at each of the 49 sample points.

Soil thickness measurements

Thickness of soil horizons was measured using a refraction seismic method (RSM) that measures the velocity at which a seismic wave propagates through subterranean material, such as soil, weathered bedrock, or hard bedrock (e.g., Haeni 1986; Meju et al. 2003). Higher seismic primary-wave velocities indicate material of higher density, typically quantifying the strength or competency of the material. This allowed measurements of the depth to competent or weathered bedrock beneath the upper soil horizons (below A + C horizons) and the depth to unweathered hard bedrock (below Cr horizon; McCann et al. 1988; Gasch et al. 2002). Seismic geophones were placed at 6 m intervals along seven parallel east–west transects that overlapped with all 49 sample points. Using a digital, distributed, 24-bit instrument, seismic velocities were recorded from the energy produced from an impact tool placed between each set of successive geophone locations. Results were provided as a profile of RSM values with depth along each transect. We used RSM velocity values to indicate lower boundaries of A + C and Cr soil horizons (1,000 and 3,500 m/s, respectively), based on standard values (McCann et al. 1988) and adjusted for granitic-based soils (Gasch et al. 2002) and calculated the Cr horizon thickness by subtraction of the A + C horizon from total soil depth.

We compared the RSM velocity estimates of the A + C and Cr horizon thickness against measurements from a tile probe, a field instrument commonly used by foresters. The probe was a long (up to 2 m) steel rod with a crossbar that was shoved into mineral soil using the downward force equal to the weight of the tile probe operator. To reduce variation in downward force applied, the same two people of similar height and weight operated the probe for the calibration and plot data collection. We inserted the tile probe at five randomly selected points within 2 m of each grid point and used the maximum value from the five samples to minimize the influence of cobbles. We calibrated tile probe measurements by digging soil pits at five sites within 300 m of the study site. Calibration sites were chosen to represent a range of perceived soil depths from deep to shallow based on observed surface physiographic features. We selected deep soil sites where there was no visible surface bedrock or evidence of geomorphic processes (e.g., sediment accumulation, mass wasting), and thin soil sites based on the presence of one or more of the following features: high percent cover of surface bedrock outcrops, ridges or benches, or forest openings with no A horizon. At each site, five tile probe measures were taken 40 cm apart along a 2 m transect. The area surrounding the tile probe measurements was then excavated by shovel, taking care to not step on or pile soil on one side of each soil pit. Once each pit was excavated to the bottom of the Cr horizon, the depth from the soil surface to the boundary between A + C and Cr soil horizons was measured in five locations along the soil pit and averaged to one value.

Statistical analysis

Stand variables

We used Pearson's correlation to examine the association between upper and lower soil thickness and seismic and tile probe measures of soil thickness. We used linear regression to estimate thickness of the A soil horizon (PROC REG, SAS Version 9.1) with the average of the five probe measurements as the predictor variable and soil thickness via excavation as the response variable. We also used linear regressions to evaluate the relationships between tile probe and seismic soil thickness estimates using the top 50 cm in a first analysis and lower 50–150 cm of soil in a second analysis (as measured using seismic methods). We used multiple regressions with a forward stepwise procedure to select independent predictors (A + C and Cr soil horizon thicknesses; included in model if $P = 0.10$) of stand variables (total tree basal area, canopy cover, shrub cover, basal area of white fir). All variables were evaluated for normality, homoscedasticity, and independence of residuals. All conifer species, with the exception of white fir (normal distribution), were analyzed using logistic regression (see below) due to their non-normal distribution. We tested for serial correlation using a Durbin–Watson statistic and multicollinearity by examining correlations between independent factors and calculating the Variance Inflation Factor for each significant factor (Statistica 2003).

Regeneration

We used logistic regression to relate selected soil factors to the occurrence of red fir, incense-cedar, sugar pine, and Jeffrey pine trees as well as seedlings of each species (Jeffrey pine seedlings were excluded due to inadequate sample size). We selected A + C and Cr horizon thickness in our analyses of the occurrence of each tree species (red fir, incense-cedar, sugar pine, Jeffrey pine) and incense-cedar and sugar pine seedlings. In addition to soil horizon thickness, we included soil moisture and temperature in our analyses of white fir and red fir seedling occurrence, and soil moisture in our analyses of incense-cedar and sugar pine seedling occurrence, because these variables were important predictors of seedling occurrence for conifer species at our study site (Gray et al. 2005). To reduce model over-fitting, we only included significant ($P < 0.05$) predictors in our logistic regression analyses, and tested for multicollinearity by examining potential correlation between independent factors in each model. For each significant parameter in the logistic regression model, we calculated odds-ratios and their confidence intervals based on a Quasi-Newton estimation that approximates the second-order derivatives of the retrospective loss function (Statistica 2003). The odds-ratio estimates were interpreted as the odds of occurrence of a tree species given a one unit change in a soil parameter (e.g., A + C horizon thickness) after being adjusted for the effects of other soil parameters in the model. Odds-ratios provide information regarding the relative importance of soil parameters on tree or seedling occurrence and do not imply cause and effect relationships between these variables. We used a sensitivity analysis of each treatment type to evaluate the performance of the reduced logistic regression model and assess model accuracy in successfully predicting occurrence of tree species among sample points (Hosmer and Lemeshow 2000). Unless otherwise noted, all statistics were conducted with Statistica 6.1 (StatSoft Inc., Tulsa, OK, USA) and an α level of 0.05.

Results

Thickness of A + C and Cr horizons were not correlated (r = -0.171, P = 0.240) and were highly variable at Teakettle (Table 1, Fig. 1). Total basal area (Fig. 2) and canopy cover were positively related to A + C horizon thickness (Table 2), and shrub cover was positively related to Cr horizon thickness (Fig. 3). Basal area of white fir was positively related to A + C horizon thickness (Table 2). The probability of incense-cedar tree occurrence increased with greater A + C horizon thickness (Table 3), but there was no relationship between A + C or Cr horizon thickness and the occurrence of sugar pine ($\chi^2 = 2.739$, $df = 1$, $P = 0.098$), Jeffrey pine ($\chi^2 = 1.711$, $df = 1$, $P = 0.191$), or red fir ($\chi^2 = 1.510$, $df = 1$, $P = 0.219$). The reduced logistic regression model correctly classified 62 and 75% of incense-cedar presence and absence, respectively.

Ninety-three percent of censused conifer seedlings were either white fir or red fir, and spatial variability in seedling abundance was high for all species (Table 1). The probability of occurrence of white fir seedlings increased with soil moisture and decreased with soil temperature (Table 3). The reduced logistic regression model correctly classified 44 and 81% of white fir seedling presence and absence, respectively. The probability of occurrence of red fir increased with Cr horizon thickness and decreased with soil temperature (Table 3). The reduced logistic regression model correctly classified 45 and 95% of red fir seedling presence and absence, respectively. The probability of occurrence of incense-cedar ($\chi^2 = 1.571$, $df = 1$, $P = 0.250$) and sugar pine ($\chi^2 = 1.701$, $df = 1$, $P = 0.192$) seedlings were not associated with horizon thickness or soil moisture. Ninety-eight percent of all conifer seedlings were restricted to microsites with soil temperatures ≤17°C (67% of microsites), and no seedlings of any species were found in microsites with soil temperatures exceeding 21°C (14% of microsites).

Thickness of the A + C horizon as measured by tile probe and seismic methods were positively correlated (r = 0.692, P < 0.001). There was a

Table 1 Mean (±SE), percent of total, and range of stand structure variables measured (July–August 2002) in Teakettle Experimental Forest (Fresno County, CA, USA)

Stand or soil variable	Mean (±SE)	%	Range
Tree basal area (m^2/ha)			
Total	53.1 (5.2)		
White fir	30.9 (1.9)	58.1	
Red fir	5.6 (0.9)	10.6	
Sugar pine	10.1 (1.2)	19.0	
Incense-cedar	4.2 (0.7)	7.9	
Jeffrey pine	2.3 (0.3)	4.3	
Seedling density (n/ha)			
Total	2,984 (1,661)		0–310
White fir	1,426 (726)	47.8	0–133
Red fir	1,352 (936)	45.3	0–176
Sugar pine	117 (42)	2.6	0–4
Incense-cedar	80 (27)	3.9	0–3
Jeffrey pine	11 (11)	0.4	0–2
A + C horizon thickness (cm)	48 (5)		5–137
Cr horizon thickness (cm)	105 (7)		1–208
Litter depth (cm)	1.9 (0.2)		0–6.2
Hemispherical canopy cover (%)	79.8 (1.0)		60.5–89.6
Shrub cover (%)	18.9 (4.0)		0–90
Herbaceous plant cover (%)	5.3 (1.8)		0–59
Soil volumetric water content, 0–15 cm (%) August 2002	2.95 (0.09)		1.73–4.18
Soil temperature (°C) August 2002	16.9 (0.6)		12.0–27.2

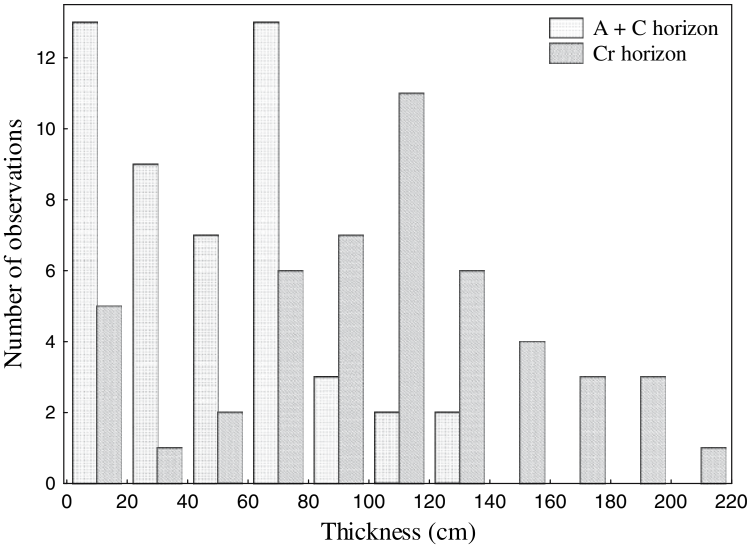


Fig. 1 Histogram of A + C horizon and Cr horizon soil thickness in Teakettle Experimental Forest

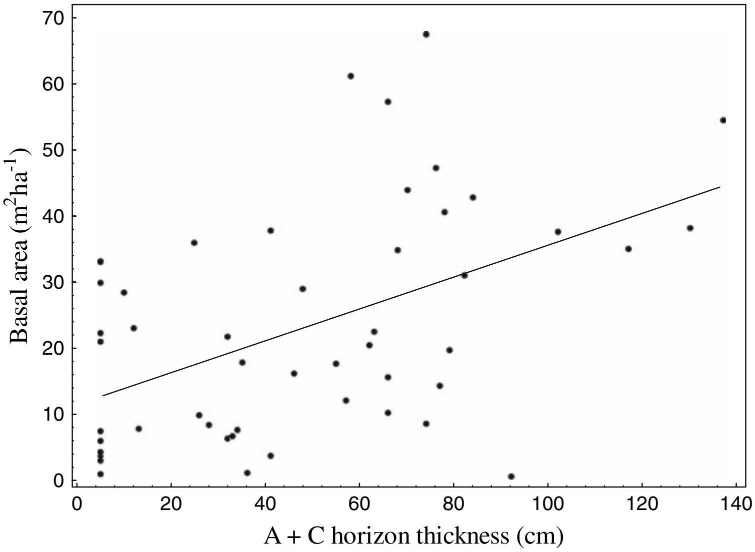


Fig. 2 Plot of relationship between A + C horizon thickness and basal area

Table 2 Best linear regression models for basal area, shrub cover, and canopy cover in relation to soil horizon thickness in Teakettle Experimental Forest

Variable	Predictors	Coefficient estimate	Coefficient standard error	Predictor *P*	Partial R^2	Overall regression	
						R^2_{adj}	*P*
Basal area	A + C horizon thickness	0.175	0.071	0.018	0.27	0.30	<0.001
Canopy cover	A + C horizon thickness	0.093	0.025	<0.001	0.21	0.21	<0.001
Basal area of white fir	A + C horizon thickness	0.446	0.132	0.002	0.18	0.18	0.002
Shrub cover	Cr horizon thickness	0.209	0.079	0.011	0.11	0.11	0.011

Fig. 3 Plot of relationship between Cr horizon thickness and shrub cover

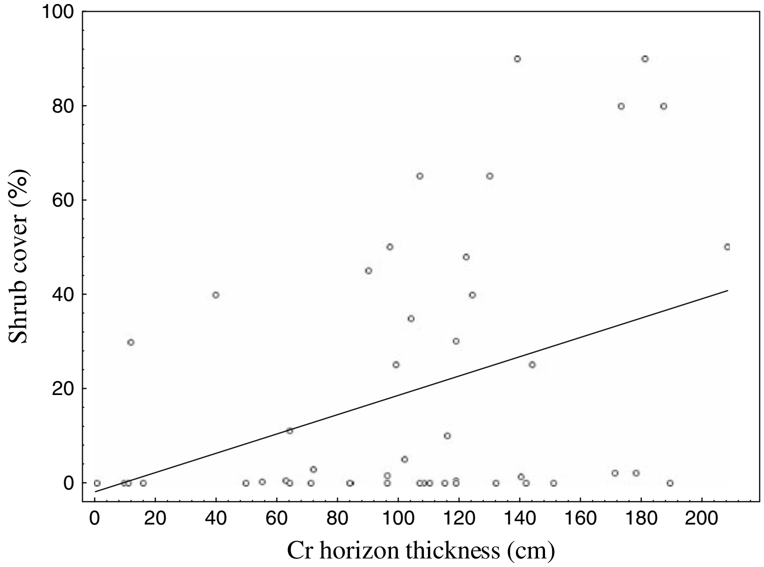


Table 3 Results of logistic regression models indicating soil variables associated with the occurrence of tree species and seedlings in Teakettle Experimental Forest

Species	Independent variable	Estimate (SE)	χ^2	Odds ratio[a] (95% CI)	*P*
Trees					
Incense-cedar	A + C horizon	0.027 (0.011)	6.328	1.3 (1.1–1.5)	0.012
Seedlings					
White fir	Soil moisture	1.68 (0.72)	5.364	5.3 (1.2–22.9)	0.021
	Soil temperature	–0.36 (0.14)	6.587	0.7 (0.5–0.9)	0.010
Red fir	Cr horizon	0.02 (0.01)	4.637	1.2 (1.0–1.4)	0.031
	Soil temperature	–0.40 (0.18)	4.974	0.7 (0.5–1.0)	0.026

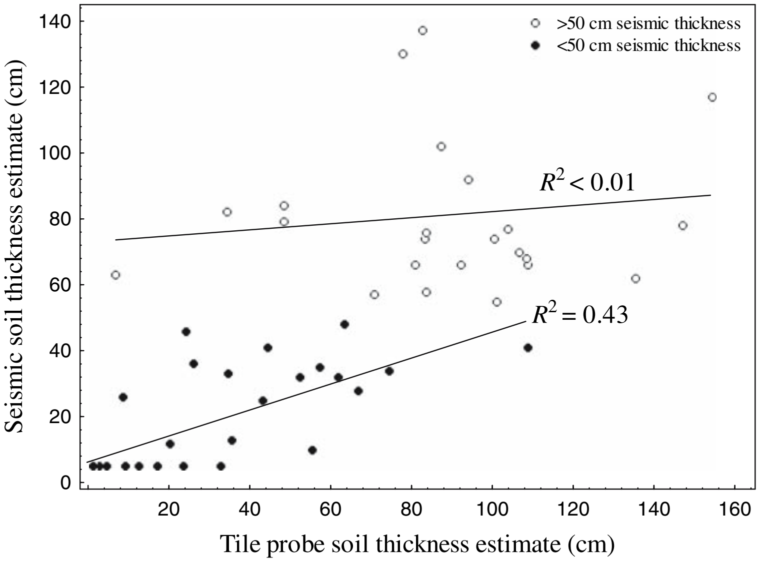
[a] Effect of a 10-cm increase in soil horizon thickness or one unit increase in soil moisture or temperature

positive relationship between tile probe and seismic thickness measures using the top 50 cm of soil from seismic estimates ($\beta = 0.676 \pm 0.150$, $F_{1,24} = 20.182$, $R^2_{\text{adj}} = 0.434$, $P < 0.001$) but not the bottom (>50 cm) portion of this soil ($F_{1,21} = 0.127$, $R^2_{\text{adj}} = 0.006$, $P = 0.725$; Fig. 4).

Discussion

Our study was limited to a single forest stand and represents an investigative study of the relationship between soil and stand variables within a stand. Results should be viewed with caution and with attention to limitations in the size of the study area and soil measurement techniques. Thickness of A + C horizon and not Cr horizon were important for overstory stand composition in our 4-ha stand at Teakettle. This may be largely due to the overstory dominance of white fir at our study site, a shade-tolerant species with roots located primarily in the upper soil horizon (Laacke 1990). Greater thickness of organic and mineral layers in the upper soil horizons may hold more soil moisture that can be important for more water-limited and shade-tolerant tree species, white fir, red fir, and incense-cedar, which dominate our study site (Gray et al. 2005). Additionally, increased A + C horizon thickness may provide tree roots with increased rooting volume and access to a greater diversity of ectomycorrhizal networks that can increase water uptake for symbiotic tree roots (Bruns 1995; Izzo et al. 2005). In the northern Sierra Nevada, white fir and incense-cedar frequently grow in deeper soils, while Jeffrey pine is often observed on

Fig. 4 Plot of relationship between tile probe and seismic estimation of A + C and Cr horizon thickness



shallow soils with increased cover of surface rock (Vasek 1978). In the southern Sierra Nevada, Jeffrey pine productivity was not limited by upper horizon thickness if underlain by a thick layer of weathered bedrock (Witty et al. 2003). At Teakettle, white fir and incense-cedar were associated with thicker A + C horizon soils, although we did not detect an association between Jeffrey pine occurrence and shallow A + C horizon or deep Cr horizon soils, possibly due to the infrequent occurrence and small sample size of Jeffrey pine at our study site.

White and red fir seedlings were associated with cooler (both species) and moister (white fir) soils at Teakettle, although the percentage of logistic regression models that correctly classified the presence of seedlings of either species was low (<50%). These results support previous observations that white and red fir seedlings grew more favorably (Barbour et al. 1990) or were more frequently encountered (Gray et al. 2005) in microsites with relatively high soil moisture and low direct solar radiation. At our study site, red fir seedlings were associated with thicker Cr horizon microsites, in contrast to our hypothesis that the thickness of the A + C horizon is more important than deeper weathered bedrock for regeneration of this species. In red fir forests of the Sierra Nevada, red fir seedling and sapling cover was correlated with total soil depth in clearcut areas where regeneration was defined as 'very slow' (Barbour et al. 1998). In the southern Sierra Nevada, roots of ponderosa pine (*P. ponderosa* Laws.) seedlings have been shown to penetrate mineral soil into weathered bedrock within 2 years of establishment (Witty et al. 2003), but similar work has not been conducted on red fir root dynamics. In a growth chamber experiment, roots of red fir seedlings averaged 34 cm depth in the first six months of growth (Barbour et al. 1990). At Teakettle, we've found red fir seedlings ($\bar{x} = 35$ cm height) with an average root depth of 58 cm (A.N. Gray and H.S.J. Zald, personal observation) and suspect some seedlings may penetrate weathered bedrock to extract water in the first several years of growth. Interestingly, white fir seedlings at Teakettle ($\bar{x} = 38$ cm height) also had relatively long roots ($\bar{x} = 53$ cm depth), indicating that weathered bedrock could be an important medium for water uptake and survival of some white fir seedlings. Further research is needed to understand the belowground mechanisms that influence conifer regeneration in Sierra Nevada mixed-conifer forests.

In accord with our predictions, shrubs were positively related with thickness of the Cr horizon composed of decomposed granite and very low organic material. Shrubs in water-limited forests, such as *A. patula* Greene, extract soil water from the upper soil horizons (Royce and Barbour 2001) but shift to lower bedrock-derived soil late in the growing season when upper soil horizons are dry (Rose et al. 2002). Our study site was dominated primarily by *C. cordulatus* Kellogg, a nitrogen-fixing shrub that occurs primarily on soils exceeding 1 m depth at Teakettle (North et al. 2002). Several species of *Ceanothus* have deep (>2 m) roots that may extract soil moisture from lower soil horizons (Conrad et al. 1985), and potentially tap into deep ectomycorrhizal networks within bedrock material (Bornyasz et al. 2005). In southern California, roots of *C. greggii*. Gray and other chaparral shrubs penetrated depths exceeding 4 m (Sternberg et al. 1996) and roots of *C. leucodermis* Greene exceeded 6 m in depth (Conrad et al. 1985). At Teakettle, *C. cordulatus* Kellogg roots have been found at 2 m depths, and we suspect these deeper roots can extract soil moisture from weathered bedrock (North and Zald, personal observation).

Seismic and soil penetration methods provided similar estimates of mineral soil thickness above 50 cm, but there was no relationship between these methods below this depth. In our study, seismic estimates of mineral soil thickness <20 cm were highly variable (Fig. 4), and possibly inaccurate due to poor refraction propagation in shallow soils. In contrast, tile probe measurements were fairly accurate for shallow soils, but in three of our five pilot soil pits, probes provided poor estimates when soil thickness exceeded 50 cm. Unlike soil penetration methods, seismic methods provided estimates of both mineral soil and decayed bedrock thicknesses at total depths exceeding 250 cm. Although seismic estimation of soil horizon thickness has been frequently used in geologic and hydrologic studies, it has rarely been used in forest research. In this study, we found that visual surface conditions and tile probe estimates of soil thickness can be misleading because ‘shallow’ areas may have a thick layer of weathered bedrock. In moisture-limited forests, weathered bedrock is a potential rooting medium for shrubs, red fir seedlings, and Jeffrey pine and only RSM could potentially measure its thickness.

Our study suggests that both soils and weathered bedrock zones are important for shaping patterns of stand composition and regeneration within a single Sierra Nevada mixed-conifer forest stand. This is particularly the case where mineral soil is thin and weathered bedrock is relatively thick and provides rooting substrate for deep-rooted tree and shrub species. Patches of shrubs and low-density Jeffrey pine may occur on apparently shallow soil conditions, but these areas may be underlain with a relatively thick layer of water-holding weathered bedrock. More extensive studies comparing soil thickness and vegetation are needed to better understand the association between above ground vegetation composition and soil horizon characteristics and thickness.

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