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Root System Development of Juvenile Ponderosa Pine as Influenced by Soil Type and Nutritional Augmentation

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Abstract

A comparison of the capacities of granitic and andesitic soils, with and without nutritional augmentation, to promote above- and below-ground development of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) seedlings was conducted. Shoot dimensions and dry weight along with root system length and weight within both the coarse and fine fractions were all significantly enhanced in granitic soils compared to an andesitic one, and seedlings grown in the former had far more short roots and ectomycorrhizae as well. For both shoots and roots, the magnitude of these growth enhancements was somewhat more pronounced in a less weathered granitic soil than in a more weathered one such that at the conclusion of the study, total shoot biomass of seedlings grown in the andesitic soil averaged 38% of that produced in the less weathered granitic one and 47% of that in the more heavily weathered granitic soil, while such comparisons regarding that of the roots revealed values of 28% and 34%, respectively. Fertilization at the onset of the study with either N or P or N+P had little capacity to compensate for the growth deficiencies in either above- or below-ground seedling tissues attributable to the andesitic soil, and its influences in the granitic soils were muted and largely ephemeral. Shoot growth was well correlated with root system length and weight and at least moderately so with short root and mycorrhizal counts, although such counts were commensurate with stronger regression models primarily when limited to the fine rather the coarse root size fraction.

Keywords: Forest soils; Forest fertilization; Seedling development; Shoot growth; Root growth; Short roots; Ectomycorrhizae; Ponderosa pine; *Pinus ponderosa*

Introduction

Of the multitude of species found in the coniferous forests of the western USA [1,2], perhaps none is more iconic than ponderosa pine [3,4], a reflection of its ecological and economic importance where it resides but also its extensive natural range, which is not only expansive geographically but encompasses a broad array of sites including those that are too xeric for most other native conifers to inhabit [2,5-7]. Whether extant in pure stands or as a component of mixed compositions, and both cases are common [8-11], in mature form it is renowned for its deep, well-developed root system that renders it wind firm on exposed sites as well as capable of enduring exceedingly dry ones [6]. In the seedling stage, a critical attribute permitting its successful establishment on drier substrates is the quick extension of the taproot needed to provide anchorage and access to moisture before it expends resources on lateral root development [12]. Furthermore, like all pines, it is dependent upon ectomycorrhizal associations [13] whether in the juvenile [14] or an advanced [15] developmental stage, and a reasonable presumption is that such symbioses provide for enhanced nutrient uptake, water relations, and deterrence of pathogens, the same benefits they deliver for other species and genera [13,16]. Implicit in the broad array of sites that ponderosa pine inhabits is that it grows in a wide variety of soils as well. In the Sierra Nevada alone, two diverse but distinct soil classes as distinguished by parent material are pertinent, specifically one of granitic and the other of andesitic origin but with each encompassing multiple soil series. Although distinctive regarding several characteristics other than geologic origin, perhaps most notable is that the soils of the former frequently have a relatively coarse texture, in part reflecting that they are not highly developed, while those of the latter exhibit high phosphorus fixation [17]. It is plausible that these and other differences among the diverse soil types serving as substrates for this species exert profound influences on its rooting characteristics, but this aspect of ponderosa pine development remains largely unknown to date.

The study reported here was designed to provide for quantitative assessment of the effects of soil type on root system development, including mycorrhizal formation, in juvenile ponderosa pine. Additionally, it incorporated varied nutritional augmentation of the selected soils in order to provide insight into the possible nutrient deficiencies inherent in each soil type through evaluation of the ameliorative effects of each amendment. Regression analyses were employed to assess the relationships between root system development as influenced by treatment and the development of above-ground seedling tissues.

Materials and Methods

Experimental setup

Three soils served as the growth media incorporated into the study. The first one, hereafter designated as the DG soil, was collected from a forested site (39°14′40″N, 119°52′50″W) in the Carson Range of the eastern Sierra Nevada bearing the Marla soil series [18], which consist of sandy, mixed Aquic Cryumbrepts derived from colluvium of decomposed granite. The second was also of the Marla series and was collected nearby, but it was more highly weathered and thus will be referred to hereafter as the WDG soil. The third type, designated herein as the AD soil, was collected from a forested, eastern Sierran

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site (39°27′15″N, 120°12′30″W) bearing the Waca soil series [19], a loamy-skeletal, mixed, frigid Andic Xerochrept derived from andesitic lahar/tuff. In each case, soil was collected from the upper 10 cm of the mineral profile, sieved through a No. 10 (2.0 mm opening) screen, and thoroughly homogenized. Thus prepared, each soil was then loaded into 60 Spencer-Lemaire Rootrainer containers (Spencer-Lemaire Industries Ltd., Edmonton, AB, Canada) of dimensions 7.6 × 7.6 × 25.4 cm.

Each container was sown with four equally spaced, half-sib ponderosa pine seeds (El Dorado County, CA, USA seed source). Presowing treatments consisted of a 24-hour cold water soak followed by stratification for 30 days at 3°C, and both prior to and immediately following stratification the seed coats were sterilized by immersion in 10% H_2O_2 for 10 minutes followed by a tap water rinse of 10 minutes. Upon sowing, deionized water mists were applied three times daily until germination, which occurred within approximately one week, and the seedlings were thinned to one per container soon after germination was complete. Thereafter, irrigation consisted of the application of deionized water as needed to maintain soil moisture conducive to seedling growth.

Within each soil type, fertility treatments were imposed by one-time applications of nutrient amendments, which were accomplished immediately following the thinning of the seedlings. In addition to an unfertilized control (UF), the treatments entailed a N application, accomplished by adding to each appropriate container 20 ml of 0.135 M $(NH_4)_2SO_4$; a P application using 20 ml of 0.071 M $Ca(H_2PO_4)_2$; and a N+P application consisting of 10 ml of 0.270 M $(NH_4)_2SO_4$ plus 10 ml of 0.142 M $Ca(H_2PO_4)_2$. These nutrient additions equated to fertilization at the rate of 200 kg N ha^{-1} as $(NH_4)_2SO_4$, 117 kg P ha^{-1} as $Ca(H_2PO_4)_2$, and 200 kg N ha^{-1} as $(NH_4)_2SO_4$ plus 117 kg P ha^{-1} as $Ca(H_2PO_4)_2$, respectively. Within each soil type, the individual fertilizer solutions were applied to 15 containers with 15 additional containers dedicated to the unfertilized control.

Individual seedling containers, of which there were 180 in total at the outset of the study with each of the 12 combinations of soil type and fertility treatment represented by 15 replicate containers, were arranged randomly in the greenhouse with periodic rearrangement as needed to ensure that all seedlings were subjected to a similar growing environment. For the duration of the experiment, the greenhouse temperature averaged 21.5°C with a daily maximum average of 29.9°C and a minimum average of 16.1°C, while relative humidity averaged 30.1% with maximum and minimum averages of 48.1% and 17.1%, respectively. The daily maximum average photosynthetically active radiation was 1163 mmol $m^{-2}d^{-1}$ with a daily mean excluding nighttime hours of 507 mmol $m^{-2}d^{-1}$.

Seedling measurements

Dated from the sowing of the seed in the containers, the duration of the study was 42 weeks, which encompassed an initial harvest for assessment of shoot and root development 18 weeks after sowing followed by two more at 12 week intervals and with each of the three entailing measurements conducted on five randomly selected seedlings of each combination of soil type and fertility treatment. Immediately prior to each of the harvests, shoot height and diameter at the root collar of the selected seedlings were measured and the shoots were then detached from the root systems, dried at 75°C for 72 hours, and weighed. At the initial harvest, the shoots were weighed intact, but thereafter, they were divided into stem and foliar components which were weighed separately before eventually being totaled. For every harvest, the root systems were extracted from the soil, and following a thorough washing, their ectomycorrhizal development was quantified. This was accomplished by counting all short roots, tallying those with a mycorrhizal infection identified through visual recognition, with magnification as needed, of the characteristic monopodial, bifurcate, or coralloid morphology or an obvious fungal mantle, and expressing the number of colonized short roots as a percentage of the total short root count [20]. Comparison of the mycorrhizae thus quantified with documented descriptions of those previously observed on ponderosa pine provided for tentative identification of the mycobionts colonizing the seedlings of the present study. Further assessment of root system development entailed measurements of root length excluding that of the short roots and then drying and weighing all root tissues in the manner noted above concerning the shoots. However, specific to root systems, the entire quantification of their development, including short root tally, ectomycorrhizal colonization, length, and dry weight, was segregated into that of the coarse (≥ 2.0 mm diameter) and fine (<2.0 mm diameter) fractions before eventually being combined for purposes of calculating root totals, total seedling dry weight, and shoot/root ratio. An additional calculation derived from measurements specific to the second and third harvests was the percentage of total seedling weight accounted for by that of the foliage.

Statistical analyses

All data derived from this study were analyzed using repeated-measures mixed-model analysis of variance (ANOVA) to test for the effects of soil type and fertility treatment plus that of harvest timing along with all possible interactions. This analysis incorporated both the compound symmetry covariance structure and the first-order autoregressive structure. For each variable, the covariance structure relied upon was that providing the lowest value for Akaike's Information Criterion (bias-corrected version, AICC). Prior to analysis, the arcsine transformation was performed on all percentage data, and main and interaction effects were considered significant only when $p \leq 0.05$ according to the F test. With $\alpha = 0.05$ designated, the least significant difference (LSD) test was subsequently employed to distinguish differences among the individual means for each variable.

To investigate linkages between root system development and that of the shoots, a series of simple linear regression models were computed that paired measurements of the former as independent variables with dependent variables entailing those specific to the latter. These models coupled, in all possible combinations, root length and weight, short root count, and colonized short root count and percentage, all segregated into coarse and fine fractions as well as in aggregate, with shoot dimensions and dry weight plus total seedling weight and shoot/root ratio. For every model, the values incorporated into each pairing of independent and dependent variables were derived from the same harvest, and the models specific to the second and third harvests included ones with the dependent variables of stem weight plus foliage weight and percentage along with the total shoot weight included in initial harvest models. Regression models were considered significant only when $p \leq 0.05$ according to the F test, and particular emphasis was placed on gauging the strength of the relationships between the independent and dependent components of significant models. All statistical analyses were performed using SAS version 9.3 (SAS Institute, Inc., Cary, NC).

Results

Shoot dimensions

According to ANOVA, seedling height and diameter were each significantly influenced by soil type (both $p < 0.0001$) and the time

of harvest (both $p<0.0001$) along with the soil × harvest interaction ($p=0.0213$ and $p<0.0001$, respectively), while for stem diameter alone the soil type × fertility treatment interaction was influential ($p=0.0014$) as well (Table 1). As for differences among means at the initial harvest as disclosed by the LSD test, seedlings grown in the DG soil amended with either the N or P fertilizers, which numerically exhibited the greatest height growth of any treatment combination at the time, were significantly taller than those grown in this soil but of the UF or N+P fertility treatments, were taller than those grown in the WDG soil without nutritional augmentation, and were taller than seedlings grown in the AD soil regardless of fertility treatment. Other height disparities at the first harvest consisted of taller seedlings produced by the WDG

			Dimensions		Weights		
Harvest	Soil	Fertilizer	Height (cm)	Diameter (mm)	Stem (g)	Foliage (g)	Total (g)
1	DG	UF	6.1bcd	1.6bcd	-	-	0.48bcd
		N	7.8a	1.9ab	-	-	0.72a
		P	7.8a	1.8abc	-	-	0.63ab
		N+P	6.2bcd	1.7abcd	-	-	0.52abcd
	WDG	UF	6.2bcd	1.4d	-	-	0.46bcd
		N	7.7ab	2.1a	-	-	0.73a
		P	6.9abcd	1.5cd	-	-	0.54abcd
		N+P	7.3abc	1.6bcd	-	-	0.59abc
	AD	UF	5.1d	1.4d	-	-	0.27e
		N	5.7cd	1.4d	-	-	0.36cde
		P	5.9cd	1.6bcd	-	-	0.36cde
		N+P	6.1bcd	1.4d	-	-	0.33de
2	DG	UF	9.0abcd	2.6bcde	0.33abcd	0.75abcd	1.08bc
		N	8.2bcd	2.5bcde	0.32bcd	0.71bcd	1.03bc
		P	9.9ab	3.0abc	0.41ab	0.81abc	1.22ab
		N+P	10.9a	3.6a	0.53a	1.09a	1.62a
	WDG	UF	8.4bcd	2.5bcde	0.28bcde	0.66bcde	0.94bcd
		N	9.0abcd	3.1ab	0.44ab	0.99ab	1.43ab
		P	9.6abc	2.7bcde	0.39abc	0.86ab	1.25ab
		N+P	9.0abcd	2.8bcd	0.34abcd	0.76abcd	1.10abc
	AD	UF	8.0bcd	2.3cde	0.20cde	0.44de	0.64cd
		N	6.9d	2.0e	0.14e	0.35e	0.49d
		P	7.5cd	2.3cde	0.14e	0.46de	0.60cd
		N+P	6.9d	2.1de	0.15de	0.48cde	0.63cd
3	DG	UF	10.5ab	3.8abc	0.59ab	1.06ab	1.65ab
		N	11.5a	4.0ab	0.64ab	1.52a	2.16a
		P	11.0ab	3.4abcd	0.59ab	1.17ab	1.76ab
		N+P	11.8a	4.1a	0.75a	1.36a	2.11a
	WDG	UF	10.4ab	3.2bcd	0.45bcd	0.78bc	1.23bcd
		N	9.3abcd	3.5abcd	0.59ab	1.25ab	1.84ab
		P	10.1abc	3.7abc	0.50abc	0.87bc	1.37bc
		N+P	10.6ab	3.6abc	0.57ab	1.24ab	1.81ab
	AD	UF	7.8cde	2.7de	0.24de	0.57cd	0.81cde
		N	7.1de	2.0ef	0.20de	0.43cd	0.63de
		P	8.6bcde	2.9cd	0.36cde	0.83bc	1.19bcd
		N+P	6.1e	1.6f	0.10e	0.23d	0.33e

Table 1: Shoot dimensions and dry weights of ponderosa pine seedlings as influenced by soil type and fertilization [1]. For each combination of measurement variable and harvest, means sharing a common letter do not differ significantly at $\alpha=0.05$ according to the LSD test; each mean is based on values from five seedlings (n=5).

soil and N fertilizer combination than those grown in the AD soil with any fertility treatment except N+P along with taller ones grown in the former but augmented with N+P than seedlings from the unfertilized AD soil. Concurrent diameter disparities consisted of a larger one in the WGD soil and N fertilizer combination than those of every other combination except DG soil with N, P, or N+P amendments, a larger one for seedlings grown in the DG soil with N added than those produced by either the unfertilized WDG soil, the latter fertilized with P alone, or the AD soil with any fertility treatment except P, and a larger one in the DG soil with P added than those produced by the unfertilized WDG soil or the AD soil when combined with any other than the P fertility treatment.

At the second inventory, differences in seedling dimensions disclosed as significant by the LSD test were again prevalent (Table 1). For height, the combination of DG soil and N+P fertilization, which yielded the highest value, grew taller seedlings than those produced by this soil combined with N alone, by the unfertilized WDG soil, and by the AD soil regardless of fertility treatment. Scaling downward, DG soil fertilized with P grew taller ones than the AD soil in combination with any fertility treatment except UF, and the WDG soil fertilized with P alone grew taller ones than the AD soil with either N or N+P fertilization. As for diameter growth, the highest overall value was again found in seedlings produced by the DG soil amended with N+P, which with the exception of seedlings grown in this soil but fertilized with P alone and those grown in WDG augmented with N, exceeded those associated with all other soil and fertility treatment combinations. Additional significant disparities consisted of a larger diameter in seedlings grown in the WDG soil with N added than in those grown in the AD soil regardless of fertility treatment, a larger one in the DG soil with P added than in those produced by the AD soil fertilized with either N alone or N+P, and a larger one in WDG soil augmented with N+P than in seedlings of the AD soil and N fertilizer combination.

At the final inventory, cumulative height growth in seedlings grown in the DG soil with N+P fertilization was again numerically greatest overall but only marginally exceeded that of ones grown in the same soil but with N only fertilization, and these two combinations produced significantly taller seedlings than the AD soil coupled with any fertility treatment, while those entailing the other two fertility treatments and the DG soil type along with the unfertilized WDG soil and that amended with N+P produced taller ones than the AD soil coupled with any except the P fertility treatment (Table 1). The remaining height disparities at this harvest consisted of taller seedlings in the WDG soil fertilized with P than those grown in the AD type augmented with either N or N+P and taller ones in the WDG type fertilized with N than those grown in the AD soil amended with N+P. As for final diameters, the largest overall was once again those of seedlings grown in the DG soil with N+P fertilization, which exceeded the diameters of seedlings associated with the unfertilized WDG soil or with the AD soil in its entirety. Of the remaining, and numerous, significant disparities, the stem diameter of seedlings reared in the DG soil with N fertilization also exceeded that of ones grown in the AD type without exception, that of seedlings grown in unfertilized DG soil and in WDG amended with either P alone or N+P was larger than the diameters associated with the AD type coupled with any except the P fertility treatment, those of seedlings grown in DG soil fertilized with P and WDG fertilized with N were larger than seedling diameters in the AD soil amended with either N or N+P, and within the latter soil type, diameters were larger in seedlings that received P than those receiving either N alone or N+P and were larger in unfertilized ones than those fertilized with N+P. Readily apparent in the outputs generated with both ANOVA and the LSD test was that throughout the study the AD soil type was deficient in promoting dimensional shoot growth compared to the DG and WDG soils, a deficiency exemplified by a height when averaged across fertility treatments in the AD soil of only 66% of that in the DG soil and 73% of that in WDG at the final harvest, while such comparisons regarding diameter yielded values of 60% and 66%, respectively.

Shoot weights

Like the shoot dimensions, total shoot dry weight was significantly affected by soil type and the time of harvest (both $p<0.0001$) along with the soil × harvest interaction ($p=0.0001$) according to ANOVA (Table 1). Initially, that of seedlings grown in the DG and WDG soils fertilized with N were nearly identical and numerically the heaviest, which contrasted against the shoot weights induced by unfertilized soil of either of these types along with those induced by the AD soil irrespective of fertility treatment. Other significant distinctions disclosed by the LSD test for this variable consisted of a shoot weight of seedlings grown in DG soil augmented with P that also exceeded any of those produced by the AD soil, one for seedlings grown in WDG fertilized with N+P that exceeded those elicited from unfertilized AD soil or that receiving N+P, and ones for seedlings grown in unfertilized DG and WDG soils that also surpassed that induced by unfertilized AD soil. At the second inventory, total shoot weight was greatest overall in seedlings grown in DG augmented with N+P, with the LSD test distinguishing it from those associated with both unfertilized soil of this type and that amended with N, from that induced by unfertilized WDG, and from those of seedlings grown in the AD soil coupled with any of the fertility treatments. Additionally, shoot weights induced by the DG soil with P added and by WDG amended with either N or P were greater than any associated with the AD soil as well while those induced by WDG with N+P added and by either unfertilized DG or that receiving N exceeded the weight induced by the AD plus N combination. For shoot weights at the final inventory, that of seedlings grown in the DG soil fertilized with N was numerically greatest overall but only marginally exceeded that of ones grown in the same soil but with N+P fertilization, and these two combinations produced significantly heavier shoots than unfertilized WDG, WDG fertilized with P, or by any combination involving the AD soil. Furthermore, shoots associated with unfertilized DG soil and that amended with P along with those associated with WDG augmented with either N or N+P were heavier than those of seedlings grown in AD soil coupled with any other than the P fertility treatment, the shoots of seedlings grown in WDG fertilized with P were heavier than those of seedlings grown in the AD soil amended with either N or N+P, and those of seedlings grown in either unfertilized WDG or AD fertilized with P were heavier than that induced by the AD soil amended with N+P. The overall influence of soil type on shoot development was even more evident in total weight than in dimension measurements, exemplified by values derived from the final inventory when shoot weight of seedlings grown in the AD soil amounted to only 38% of that produced in DG and 47% of that produced in WDG when averaged across fertility treatments.

When shoot weight was broken down into stem and foliage components at the second and third harvests, significant effects on both disclosed by ANOVA consisted of soil type and time of harvest (all $p<0.0001$) while foliar weight was influenced by the soil type × fertility treatment interaction ($p=0.0483$) as well (Table 1). Specific to the second harvest, the LSD test distinguished the stem weight of seedlings grown in the DG soil and N+P fertilizer combination, the highest value overall, as differing from those associated with this soil type amended with N alone, with unfertilized WDG, and with the AD type of any fertility

treatment, while the latter was also significantly reduced compared to that produced by the DG soil and P treatment combination as well as the WDG and N fertilizer combination. Furthermore, WDG with added P produced stem weight exceeding those associated with the AD soil of any fertility treatment except UF and the unfertilized DG soil plus that amended with N along with WDG augmented with N+P produced ones exceeding that produced by the AD soil with either N or P added. For foliar weight at the second harvest, the DG soil amended with N+P again produced the highest overall value which again differed from that induced by this soil fertilized with N alone, by unfertilized WDG, and by the AD soil of any fertility treatment, but WDG fertilized with either N or P were the two combinations with values also surpassing those of the latter. Nevertheless, the other disparities in foliar weight disclosed at the second harvest consisted of a higher one associated with the DG soil amended with P than any of those associated with AD soil other than that augmented with N+P plus higher ones associated with DG in combination with either the UF or N fertility treatments and with the WDG and N+P combination than the weight prevailing in the AD soil augmented with N. With stems of seedlings grown in the DG soil fertilized with N+P again the heaviest overall at the final harvest, the LSD test distinguished their weight from that prevailing in the WDG and UF treatment combination along with that of any combination involving the AD soil type and with the lower weights in the latter also contrasting against higher ones in the remainder of the treatment combinations involving the DG soil as well as those entailing WDG with either N or N+P added. Additionally, the WDG soil fertilized with P produced heavier stems than AD coupled with any other than the P fertility treatment and unfertilized WDG produced heavier ones than the AD soil fertilized with N+P. As for the final foliage weights, the highest value numerically was that associated with the DG soil augmented with N but it did not differ significantly from the weight produced by this soil with N+P added, and both of these combinations produced heavier foliage than unfertilized WDG or that amended with P along with any AD treatment combination. The remaining foliar disparities at the final harvest consisted of greater weights associated with unfertilized DG or that with P added and with WDG fertilized with either N or N+P than those produced in AD soil other than that fertilized with P plus greater ones induced by WDG coupled with either the UF or P fertility treatments along with AD in combination with P fertilization than that induced by the latter soil when combined with N+P. The overall influence of soil type on shoot weight was as evident when segregated into stem and foliage components as when considered in total, exemplified by a final stem weight when averaged across fertility treatments in the AD soil of only 35% of that in the DG soil and 43% of that in WDG, while such comparisons regarding final foliage weight revealed values of 40% and 50%, respectively.

Although total seedling weight will be addressed below, the percentage of such accounted for by foliage weight was another shoot variable for which considerable variation among treatments prevailed. At the second harvest, and in the order of the UF, N, P, and N+P fertility treatments, the values for this variable were 28, 36, 27, and 32% within the DG soil; 34, 38, 34, and 37% within the WDG soil; and 36, 37, 38, and 38% within the AD soil. Presented in the same order, those at the final harvest were 27, 34, 27, and 29% for DG; 27, 33, 26, and 34% for WDG; and 35, 36, 38, and 36% for AD. ANOVA identified soil type ($p<0.0001$), fertility treatment ($p=0.0089$), and the time of harvest ($p=0.0159$) as the significant influences on this variable, while at the initial harvest the LSD test disclosed that the percentage in seedlings grown in WDG fertilized with N, the highest overall, significantly exceeded those of seedlings grown in DG coupled with any other than the N fertility treatment, that percentages in seedlings grown in DG with added N, WDG with N+P, and the AD soil irrespective of fertility treatment exceeded those of ones grown in either unfertilized DG or that amended with P, and the percentages in seedlings grown in unfertilized WDG and that fertilized with P exceeded the percentage in seedlings of the DG and P combination. Disparities revealed at the final harvest consisted of those between seedlings grown in the AD soil fertilized with P, which had the highest overall percentage, and ones grown in unfertilized DG and that amended with P along with ones grown in unfertilized WDG and that with P added, while seedlings grown in AD with either N or N+P added had higher percentages than ones of the WDG soil type fertilized with P.

Root elongation

Significant influences on coarse root length were soil type and time of harvest (both $p<0.0001$) along with the soil type × fertility treatment interaction ($p=0.0009$) while those for fine root length were soil type and time of harvest plus the soil × harvest interaction (all $p<0.0001$) according to ANOVA (Table 2). At the initial harvest, the greatest coarse root length overall was that of seedlings grown in the DG soil fertilized with N, and the LSD test revealed that it significantly exceeded the length of those grown in unfertilized WDG plus that amended with P along with the lengths of ones grown in the AD soil regardless of fertility treatment. Additionally, the lengths produced in DG soil with P added and in WDG with N added surpassed those produced in unfertilized soil of the latter type and in the AD soil of any fertility treatment, and those produced in unfertilized DG and that amended with N+P surpassed the length in the AD soil with N+P. For fine root length at the first harvest, the longest one overall was that grown in the DG soil type with P fertilization, and the LSD test distinguished it from those grown in unfertilized DG and WDG plus the former amended with N+P along with ones grown in AD of every fertility treatment, while the fine length in WDG fertilized with N+P exceeded those in every treatment combination noted above except that entailing N fertilization of AD soil. The remaining disparities at the initial harvest consisted of longer fine root lengths in WDG fertilized with either N or P than the ones grown in unfertilized AD and that fertilized with N+P.

At the second harvest, identical coarse root lengths were found in the DG soil fertilized with N+P and in WDG with N amendment, and these constituted the highest overall values which the LSD test distinguished from those produced in the remaining combinations involving the WDG soil type plus those produced in the AD soil coupled with any of the fertility treatments (Table 2). Additionally, the coarse length produced in unfertilized DG soil exceeded that grown in WDG with N+P added and in AD with any fertility augmentation, that produced in DG with P fertilization also exceeded those produced in any fertilized AD soil, and ones produced in unfertilized WDG and AD plus the former with P addition exceeded that in the latter soil type with added N. As for fine root length at the second harvest, the longest overall was that grown in DG fertilized with N+P which exceeded the length produced in this soil with N alone along with any grown in the AD soil, while lengths in the latter were also surpassed by those produced in unfertilized DG as well as that augmented with P plus the ones grown in WDG with either N or P added. The remainder of the disparities involving length in the fine fraction consisted of longer ones in unfertilized WDG and that amended with N+P than the one extant in the AD soil augmented with P.

Coarse root length of seedlings grown in the DG soil fertilized with P was the longest overall at the final inventory, and the LSD test revealed it to surpass those grown in the WDG and AD soils regardless of fertility

			Lengths			Weights		
Harvest	Soil	Fertilizer	Coarse (cm)	Fine (cm)	Total (cm)	Coarse (g)	Fine (g)	Total (g)
1	DG	UF	3.4abc	309.8cd	313.2cd	0.05bcd	0.33bc	0.38abcd
		N	5.2a	390.4abcd	395.6abcd	0.10a	0.41ab	0.51a
		P	4.6ab	538.8a	543.4a	0.07abc	0.48a	0.55a
		N+P	3.2abc	301.2cd	304.4cd	0.05bcd	0.32bc	0.37abcd
	WDG	UF	2.0cd	296.8cd	298.8cd	0.03cd	0.28bc	0.31bcd
		N	4.8ab	424.2abc	429.0abc	0.08ab	0.40ab	0.48ab
		P	2.6bcd	417.4abc	420.0abc	0.05bcd	0.39ab	0.44abc
		N+P	3.0abcd	500.8ab	503.8ab	0.05bcd	0.38ab	0.43abc
	AD	UF	1.2cd	243.2d	244.4d	0.02d	0.20c	0.22d
		N	1.6cd	352.4bcd	354.0bcd	0.02d	0.27bc	0.29bcd
		P	1.8cd	316.0cd	317.8cd	0.03cd	0.22c	0.25cd
		N+P	0.6d	230.0d	230.6d	0.01d	0.18c	0.19d
2	DG	UF	8.6ab	891.2ab	899.8ab	0.24abc	1.35ab	1.59abc
		N	6.6abcd	618.4bcd	625.0bcd	0.18bcd	0.87bc	1.05cde
		P	8.0abc	884.8ab	892.8ab	0.27ab	1.52a	1.79ab
		N+P	9.4a	1013.6a	1023.0a	0.31a	1.53a	1.84a
	WDG	UF	6.2bcd	784.6abc	790.8abc	0.17bcd	0.87bc	1.04cde
		N	9.4a	903.0ab	912.4ab	0.29ab	0.90bc	1.19bcd
		P	5.8bcd	879.2ab	885.0ab	0.18bcd	1.14ab	1.32abc
		N+P	5.4cde	753.8abc	759.2abc	0.14cde	0.85bc	0.99cde
	AD	UF	5.8bcd	475.8cd	481.6cd	0.11de	0.50c	0.61de
		N	2.4e	449.4cd	451.8cd	0.04e	0.41c	0.45e
		P	4.8de	382.8d	387.6d	0.10de	0.54c	0.64de
		N+P	4.2de	521.2cd	525.4cd	0.09de	0.61c	0.70de
3	DG	UF	8.6abc	1523.4a	1532.0a	0.35abc	2.06a	2.41ab
		N	9.0abc	1327.4ab	1336.4ab	0.43a	1.94ab	2.37ab
		P	10.4a	1202.6abc	1213.0abc	0.39ab	1.91ab	2.30ab
		N+P	10.2ab	1341.6ab	1351.8ab	0.46a	2.11a	2.57a
	WDG	UF	7.2cd	973.8bcd	981.0bcd	0.27bcd	1.35bc	1.62bc
		N	7.8bcd	1048.4bc	1056.2bc	0.32abc	1.70ab	2.02ab
		P	7.4cd	924.8cd	932.2cd	0.33abc	1.72ab	2.05ab
		N+P	7.2cd	998.0bc	1005.2bc	0.34abc	1.68ab	2.02ab
	AD	UF	5.8de	519.8ef	525.6ef	0.15def	0.69cd	0.84cd
		N	4.0e	444.8ef	448.8ef	0.10ef	0.49d	0.59d
		P	7.8bcd	601.6de	609.4de	0.22cde	0.73cd	0.95cd
		N+P	1.2f	190.6f	191.8f	0.02f	0.26d	0.28d

Table 2: Root lengths and dry weights of ponderosa pine seedlings as influenced by soil type and Fertilization [1]. For each combination of measurement variable and harvest, means sharing a common letter do not differ significantly at α=0.05 according to the LSD test; each mean is based on values from five seedlings (n=5).

treatment (Table 2). Such was also largely true for seedlings grown in DG with N+P added in which the only exceptions were the coupling of N fertilization with the former and that of P with the latter. Other significant differences within the coarse fraction consisted of greater lengths in unfertilized DG soil and that fertilized with N than those grown in the AD soil coupled with any other than the P fertility treatment, greater ones in WDG coupled with any of the fertility treatments and in AD soil fertilized with P than those grown in the latter amended with either N or N+P, and greater ones in the UF and N fertility treatments than in the N+P treatment within the AD soil. The longest fine root fraction at the final harvest was that produced in unfertilized DG which the LSD test indicated differed significantly from those of any seedlings grown in WDG or AD soil, while other disparities involved a greater length in the DG soil fertilized with N or N+P than those associated with WDG fertilized with P or with the AD soil regardless of fertility treatment, and fine root lengths in the latter treatment combinations were also surpassed by those found in the DG soil type augmented with P and in WDG fertilized with either N or N+P. Furthermore, the length produced in unfertilized WDG or that fertilized with P exceeded those grown in the AD soil with any other than the P fertility treatment, and within the AD soil type, the P treatment produced a longer fine fraction than that of N+P. The overall influence of soil types on both coarse and fine root length was readily evident, exemplified by comparisons at the final harvest in which the coarse length in the AD soil amounted to only 49% of that extant in DG and 63% of that in WDG when averaged across fertility treatments, while such comparisons in the fine fraction yielded values of 33% and 44%, respectively.

Significant effects on total root length consisted of soil type, time of harvest, and the soil type × harvest interaction (all $p<0.0001$) according to ANOVA (Table 2). Reflecting the overwhelming contribution of fine fraction length to the total, the disparities among the various treatment combinations disclosed by the LSD test for fine length extend verbatim to total length at every harvest, and thus are not reiterated here. Regarding the overall influence of soil type on total length, again based on the measurements from the final harvest and with averaging across fertility treatments, the total within the AD soil type was only 33% of that within the DG type and 45% of that within the WDG type.

Root weights

Entailing the soil type, time of harvest, and soil type × harvest interaction effects (all $p<0.0001$), significant influences exerted on

coarse fraction, fine fraction, and total root weight were identical according to ANOVA (Table 2). At the first harvest, seedlings grown in the DG soil fertilized with N had the greatest overall coarse weight, which the LSD test deemed to be significantly different from the UF and N+P fertility treatments within this soil type, from the UF, P, and N+P treatments within the WDG type, and from all fertility treatments within the AD soil. Additional disparities consisted of a greater weight in the WDG soil fertilized with N than in its unfertilized counterpart as well as in any treatment combination involving AD soil and a greater one in DG soil fertilized with P than those prevailing in any other than the P treatment of the AD soil. For fine roots, the combination of the DG soil with P fertilization induced the greatest initial weight which differed from those produced in unfertilized DG and WDG soil along with the former amended with N+P and from the ones prevailing in any combination involving the AD soil, while the weights produced in DG fertilized with N and in WDG with either N, P, or N+P added exceeded those found in AD combinations entailing the UF, P, or N+P fertility treatments.

The second harvest revealed a coarse weight that was highest overall in seedlings grown in DG soil fertilized with N+P and which differed significantly from ones reared in this soil fertilized with N alone, in unfertilized WDG or that amended with either P or N+P, and in AD regardless of fertility treatment (Table 2). Other disparities specific to this variable consisted of weights that were higher in the DG with P and WDG with N treatment combinations than in those coupling the WDG soil with N+P or any featuring the AD soil, were higher in unfertilized DG than in any AD treatment, and were higher in DG with N added and in unfertilized WDG plus that with P added than in the AD soil fertilized with N. For fine fraction weight at the second harvest, the highest value overall was that associated with the DG soil fertilized with N+P, but it exceeded only marginally that found in this soil with P alone added, and both of these combinations produced weights that the LSD test distinguished from those produced by the DG with N combination, every combination entailing the WDG soil except that with P added, and every one involving the AD soil without exception. Additionally, the weights produced in unfertilized DG and in WDG fertilized with P also exceeded those grown in the AD soil irrespective of fertility treatment.

At the third harvest, coarse root weight was greatest overall in the DG soil with N+P added, but it differed little from that grown in this soil with N alone, and each of these combinations produced weights that differed significantly from that associated with unfertilized WDG and with the AD soil coupled with any fertility treatment (Table 2). The weight induced by the DG soil amended with P alone also surpassed those of any treatment combination involving the AD soil type, while those produced in unfertilized DG and in any fertilized WDG soil exceeded the ones grown in the AD soil coupled with any except the P fertility treatment. The remaining disparities specific to final coarse fraction weight consisted of a higher one in unfertilized WDG than those in the AD soil amended with either N or N+P along with a higher one in the latter soil type with P added than with N+P. Fine root weight at the third harvest was highest overall in the DG soil fertilized with N+P, but that in unfertilized DG was only slightly less, and both exceeded those produced in unfertilized WDG and in AD soil regardless of fertility treatment, while the DG soil with either N or P added along with WDG fertilized with any of the amendments produced higher weights than those in any treatment combination incorporating the AD soil type as well. Furthermore, the fine weight in unfertilized WDG surpassed the ones found in AD soil amended with either N or N+P. Regarding the overall influence of soil type on coarse and fine fraction root weight as exemplified by comparisons at the final harvest, the coarse weight in the AD soil amounted to only 30% of that extant in DG and 39% of that in WDG when averaged across fertility treatments, while such comparisons in the fine fraction yielded values of 27% and 34%, respectively.

Examination of total root weight at the first harvest revealed that the one in the DG soil fertilized with P was highest overall but did not much exceed that found in this soil type amended with N, and in both cases they exceeded those produced in unfertilized WDG and in the AD soil irrespective of fertility treatment, while the weight produced in WDG amended with N also surpassed those in the AD soil except that fertilized with N and those in WDG amended with either P or N+P surpassed the ones found in unfertilized AD and that with N+P added (Table 2). At the second harvest, total weight in the DG soil with N+P was greatest overall, and the LSD test distinguished it from that in this soil fertilized with N alone, from the ones in WDG of every fertility treatment other than P alone, and from those in the AD soil type without exception. Additionally, total weight in DG soil fertilized with P also exceeded that in this soil amended with N, in WDG coupled with either the UF or N+P fertility treatments, and in the AD type in its entirety, while those in the latter were surpassed as well by the weights in unfertilized DG and in WDG with the P amendment. One other significant disparity specific to total weight at the second harvest entailed a higher one in WDG than in AD soil with N added to both. For total weight at the final harvest, the highest value overall was that found in DG soil fertilized with N+P, which surpassed those found in unfertilized WDG and all treatment combinations involving AD soil. Totals associated with the UF, N, and P fertility treatments within the DG soil and with the N, P, and N+P treatments within the WDG soil exceeded those within any AD treatment combination as well, and that found in unfertilized WDG did so relative to the weights in the AD soil fertilized with either N or N+P. As for the overall influence of soil type on total weight, again based on the measurements from the final harvest and with averages encompassing all fertility treatments, the total within the AD soil type was only 28% of that within the DG type and 34% of that within the WDG type.

Short root and mycorrhizal formation

Within the coarse root fraction, the total number of short roots and the number exhibiting mycorrhizal colonization were each influenced by soil type (both $p<0.0001$) and time of harvest ($p<0.0001$ and $p=0.0017$, respectively) along with the soil type × fertility treatment interaction ($p=0.0440$ and $p=0.0351$, respectively), while the percentage of short roots colonized was influenced solely by the time of harvest ($p=0.0412$) according to ANOVA (Table 3). At the initial harvest, short roots within this fraction were generally few in number compared to the counts encountered later in the study, but nevertheless, the highest overall count was that associated with the DG soil fertilized with N which the LSD test distinguished from those in unfertilized WDG and that amended with P plus the ones found in the AD soil regardless of fertility treatment. The remaining disparities for this count consisted of higher ones in the DG soil fertilized with P and WDG with N added than those in the AD soil with either N or N+P added, neither of which had any short roots at this juncture. Despite the significant effects disclosed by ANOVA for the number of colonized short roots within the coarse fraction, no significant disparities were divulged by the LSD test at the first harvest, an outcome extending to the percentage colonized despite pronounced variation among the various treatment combinations, and perhaps the most noteworthy finding regarding either is that mycorrhizae were initially absent entirely in the AD

			Coarse fraction			Fine fraction			Total		
Harvest	Soil	Fertilizer	Short roots (#)	Colonized (#)	Colonized (%)	Short roots (#)	Colonized (#)	Colonized (%)	Short roots (#)	Colonized (#)	Colonized (%)
1	DG	UF	4abc	2a	50a	637bcd	129b	20bc	641bcd	131b	20bc
		N	7a	3a	43a	857abc	184b	21bc	864abc	187b	22bc
		P	6ab	3a	50a	1201a	692a	58a	1207a	695a	58a
		N+P	4abc	3a	75a	644bcd	151b	23bc	648bcd	154b	24bc
	WDG	UF	2bc	0a	0a	794bc	316b	40ab	796bc	316b	40ab
		N	5ab	4a	80a	926ab	175b	19bc	931ab	179b	19bc
		P	2bc	1a	50a	859abc	109b	13c	861abc	110b	13c
		N+P	3abc	3a	100a	927ab	241b	26bc	930ab	244b	26bc
	AD	UF	1bc	0a	0a	548cd	103b	19bc	549cd	103b	19bc
		N	0c	0a	0a	647bcd	213b	33abc	647bcd	213b	33abc
		P	2bc	0a	0a	397d	90b	23bc	399d	90b	23bc
		N+P	0c	0a	0a	396d	103b	26bc	396d	103b	26bc
2	DG	UF	15ab	5abc	33a	2142abc	933a	44abc	2157abc	938a	43bcd
		N	10bcd	3bcd	30a	1360cd	513b	38bcd	1370cd	516b	38bcde
		P	9bcd	6abc	67a	2441a	1269a	52ab	2450a	1275a	52ab
		N+P	18a	9a	50a	2315ab	1057a	46abc	2333ab	1066a	46abc
	WDG	UF	4d	2cd	50a	1882abc	920a	49abc	1886abc	922a	49abc
		N	12abc	7ab	58a	2108abc	497b	24d	2120abc	504b	24e
		P	5cd	3bcd	60a	2226ab	986a	44abc	2231ab	989a	44bcd
		N+P	7cd	2cd	29a	1556bcd	432b	28cd	1563bcd	434b	28de
	AD	UF	5cd	2cd	40a	968d	397b	41bcd	973d	399b	41bcde
		N	3d	3bcd	100a	798d	289b	36bcd	801d	292b	36bcde
		P	3d	1d	33a	829d	493b	59a	832d	494b	59a
		N+P	4d	2cd	50a	967d	333b	34cd	971d	335b	34cde
3	DG	UF	12abc	7ab	58a	3157a	996abc	31ab	3169a	1003abc	32ab
		N	13ab	3bc	23a	2922a	1299ab	44a	2935a	1302ab	44a
		P	14ab	10a	71a	2741a	1014abc	37ab	2755a	1024abc	37ab
		N+P	17a	5abc	29a	3015a	1371a	45a	3032a	1376a	45a
	WDG	UF	6bcd	3bc	50a	2252a	1003abc	44a	2258a	1006abc	44a
		N	11abc	4bc	36a	2328a	730cd	31ab	2339a	734cd	31ab
		P	7bcd	2bc	28a	2349a	880bc	37ab	2356a	882bc	37ab
		N+P	6bcd	1c	17a	2337a	682cde	29b	2343a	683cde	29b
	AD	UF	7bcd	3bc	43a	1103b	402def	36ab	1110b	405def	36ab
		N	3cd	1c	33a	713b	278ef	39ab	716b	279ef	39ab
		P	9abcd	3bc	33a	1183b	432def	36ab	1192b	435def	36ab
		N+P	1d	0c	0a	362b	107f	29b	363b	107f	29b

Table 3: Short roots and ectomycorrhizal colonization of ponderosa pine seedlings as influenced by soil type and fertilization [1]. For each combination of measurement variable and harvest, means sharing a common letter do not differ significantly at α=0.05 according to the LSD test; each mean is based on values from five seedlings (n=5).

soil. Nevertheless, at the second harvest, the total short root count in the coarse fraction was highest overall in the DG soil fertilized with N+P which the LSD test distinguished from every other treatment combination except that consisting of the unfertilized soil of this type and the WDG soil amended with N. In turn, the count in unfertilized DG was also greater than those within the WDG treatments except that entailing added N as well as in all AD treatments, and that in WDG fertilized with N exceeded the one in unfertilized soil of this type as well as those in any fertilized AD soil. Matching the overall coarse fraction count, colonized short roots therein were most numerous overall in the DG soil with N+P added as well, but in this case it differed solely from that entailing N alone within this soil type although the other disparities specified above regarding the DG with N+P combination extended verbatim to the colonized count. As for other significant differences, the number colonized in the WDG soil fertilized with N exceeded that in any of the remaining treatment combinations involving this soil type except the one entailing the P addition as well as all of those within the AD treatments except that entailing the addition of N, while the number extant in unfertilized DG and that with P added exceeded the count found in AD soil fertilized with P. Despite the prevalence of distinctions among means divulged by the LSD test for colonized count at the second harvest, however, such distinctions regarding the percentage colonized within the coarse fraction were again entirely absent as they had been initially. At the third harvest, the DG soil amended with N+P persisted in producing the highest overall short root count, which the LSD test distinguished from those in all WDG treatments except for that featuring added N and from those in all AD treatments except for that entailing added P. Additionally, the count in DG soil fertilized with either N or P surpassed that in the AD soil with either N or N+P added and the one in unfertilized DG and in WDG with N added was greater than the overall count in the AD soil amended with N+P. For colonized short roots associated with the coarse fraction, the highest count was found in DG soil fertilized with P which the LSD test distinguished from those in all other treatment

combinations except unfertilized DG and that amended with N+P, while in turn, the colonized count in unfertilized DG exceeded those in either WDG or AD fertilized with N+P and in the latter soil with N alone added. Nevertheless, and consistent with the two preceding harvests, all disparities among the various treatment combinations in the percentage of short roots colonized were nonsignificant. The overall influence of soil type on short root development within the coarse fraction and in the mycorrhizal colonization thereof is readily evident when averages across fertility treatments at the final harvest are examined, revealing that the count irrespective of colonization in the AD soil was only 36% of that within the DG type and 67% of that for WDG, while such comparisons specific to colonized count yielded values of 28% and 70%, respectively.

Especially prolific were significant effects on short root and mycorrhizal development within the fine fraction, as the short root and colonized short root counts therein were influenced by soil type, time of harvest, and the soil type × harvest interaction (all $p<0.0001$) and the latter by fertility treatment ($p=0.0072$) and the soil type × fertility treatment ($p=0.0390$) and soil type × fertility treatment × harvest ($p=0.0269$) interactions as well, while the percentage of short roots colonized was affected by soil type ($p=0.0470$), time of harvest ($p<0.0001$), and the soil type × fertility treatment interaction ($p=0.0353$) according to ANOVA (Table 3). At the initial harvest, the highest overall count within this fraction was that associated with the DG soil fertilized with P which the LSD test distinguished from those in unfertilized soil of this type and in that with N+P added, from that in unfertilized WDG, and from the AD soil regardless of fertility treatment. Also, short roots were significantly more abundant on seedlings grown in the WDG soil fertilized with either N or N+P than on those in the AD soil coupled with any other than the N fertility treatment, and were more abundant on seedlings grown in either the DG soil fertilized with N or WDG fertilized with P than on those in AD soil amended with either P or N+P. As for the initial colonized short root count, it was again highest overall in the DG soil with P added which was not only numerically but also statistically distinctive from all of the other treatment combinations. For the percentage of short roots colonized, the DG soil with P combination once more produced the highest overall value, and with two exceptions, specifically that in unfertilized WDG and in the AD soil fertilized with N, it differed significantly from those in the other combinations as well. An additional disparity regarding the initial colonized percentage consisted of a higher one in the UF than in the P fertility treatment within the WDG soil. The prominence of the DG soil with P added within the fine fraction extended to the second harvest regarding the short root count, with the value therein distinctive from that found in this soil type fertilized with N, in WDG with N+P added, and in the AD soil irrespective of fertility treatment. Additionally, short roots were more abundant in the DG soil amended with N+P than with N alone and in the former relative to any fertility treatment within the AD soil type, and were more abundant in unfertilized DG and in WDG coupled with the UF and N fertility treatments than in any AD treatment. Although numerically superior overall, the colonized short root count at the second harvest in the DG with P combination differed little from those found in the UF and N+P fertility treatments within this soil type and in the UF and P treatments within WDG, all of which differed significantly from every remaining combination. Amounting to a clear anomaly regarding mycorrhizal development, the highest overall percentage of short roots colonized at the second harvest was found in the AD soil amended with P and it differed significantly from that occurring in the DG soil fertilized with N, from those occurring in the N and N+P fertility treatments within WDG, and from the ones prevailing in the remainder of the AD treatments. Regardless, the percentage in the DG soil with P added, which numerically was the second highest, was found to exceed those in WDG fertilized with either N or N+P and in the AD soil amended with the latter while percentages in the DG soil coupled with either the UF or N+P fertility treatments and in WDG in combination with either the UF or P treatments exceeded that found in WDG with added N. Progressing to the final harvest, the highest overall short root count within the fine fraction resided in unfertilized DG soil, but those occurring across the various fertility treatments in both this and the WDG soil type were similar and they all significantly exceeded the ones associated with any treatment combination involving the AD soil. For the final colonized count, that in the DG soil fertilized with N+P was highest overall and the LSD test distinguished it from those in WDG coupled with any other than the UF fertility treatment and in the AD soil coupled with any fertility treatment. Furthermore, the one in the DG soil with N alone surpassed those found in WDG fertilized with either N or N+P and in the AD soil without exception, the colonized counts in unfertilized DG and WDG and in either amended with P exceeded any in the AD treatments, that in the WDG with N combination surpassed the ones found in the AD soil with either N or N+P added, and the count in WDG with N+P exceeded that in AD fertilized likewise. Nevertheless, comparatively few significant disparities among treatment combinations prevailed regarding the percentage of colonized short roots at the final harvest, with the highest overall value, specifically that associated with the DG soil amended with N+P, nearly indistinguishable from that in either this soil with N alone added or in unfertilized WDG, and these three treatment combinations differed statistically only from the percentages in the WDG and AD soils fertilized with N+P. The overall influence of soil type on short root and mycorrhizal development within the fine fraction is readily apparent when averages across fertility treatments at the final harvest are compared, as the count irrespective of colonization in the AD soil was only 28% of that within the DG type and 36% of that for WDG, the colonized count in AD was only 26% of that in DG and 37% in WDG, and the percentage colonized in the WDG and AD soils was 35% overall compared to 39% in DG.

Also prolific were significant effects on short root and mycorrhizal development for the root systems in total, as the total count and colonized count were influenced by soil type, time of harvest, and soil type × harvest interaction (all $p<0.0001$) with the latter also influenced by fertility treatment ($p=0.0074$) and the soil type × fertility treatment ($p=0.0393$) and soil type × fertility treatment × harvest ($p=0.0277$) interactions, while the percentage of short roots colonized was affected by soil type ($p=0.0477$), time of harvest ($p<0.0001$), and the soil type × fertility treatment interaction ($p=0.0358$) according to ANOVA (Table 3). As for the differences among treatment combinations denoted as significant by the LSD test, the contributions of the fine fraction to the total regarding the short root count, colonized count, and percentage of short roots colonized predominated to such extent that, with one exception, the disparities among the various treatment combinations disclosed for these variables within the fine fraction extended verbatim to their respective root system totals at each of the three harvests, and thus are not reiterated here. The lone exception was the percentage colonized at the second harvest when that found in the AD soil fertilized with P, the highest overall value, exceeded the percentages in all other treatment combinations except the DG soil with either P or N+P added and the unfertilized WDG type. Additionally, the percentage found in the DG with P combination surpassed those prevailing in WDG amended with either N or N+P and AD amended with the latter, the ones in the DG soil with N+P and unfertilized WDG also

surpassed those in WDG with either N or N+P, and the percentages in unfertilized DG and in WDG with P exceeded that in the latter soil with N added. The overall influence of soil type on short root and mycorrhizal development for the seedling root systems in total, again as manifested in comparisons of the averages across fertility treatments at the final harvest, was revealed by a short root count in the AD soil that was 28% of the one in DG and 36% of that in WDG, a colonized count in AD that was 26% and 37% of those in the DG and WDG soils, respectively, and a percentage colonized in WDG and AD soils that was 35% versus one of 40% in DG.

The principal mycobiont found on the root systems in this study was probably *Suillus granulatus* (L. ex Fr.) Kuntze, a common fungus often associated with this pine in the northern Sierra Nevada [15,21] and one long known to infect its root systems [22,23]. Mycorrhizal coloration and morphology here largely conformed to that documented for this symbiont specifically [23-25], but it was not possible to confirm its identity through its sporocarps, despite their unique appearance [26], because none were found in the seedling containers at any juncture of the study, although they occur seasonally at both of the field sites where the three soils were obtained and in the vicinity of the greenhouse where the study was conducted.

Total seedling development

Combining the overall shoot and root dry weights, total seedling weights at the initial harvest in the order of the UF, N, P, and N+P fertility treatments were 0.86, 1.23, 1.18, and 0.89 g within the DG soil; 0.77, 1.21, 0.98, and 1.02 g within the WDG soil; and 0.49, 0.65, 0.61, and 0.52 g within the AD soil. Presented in the same order, those at the second harvest were 2.67, 2.08, 3.01, and 3.46 g for DG; 1.98, 2.62, 2.57, and 2.09 g for WDG; and 1.25, 0.94, 1.24, and 1.33 g for AD. At the final harvest, and again in order as above, they were 4.06, 4.53, 4.06, and 4.68 g for DG; 2.85, 3.86, 3.42, 3.83 g for WDG; and 1.65, 1.22, 2.14, and 0.61 g for AD. ANOVA identified soil type, time of harvest, and the soil type × harvest (all $p<0.0001$) as the significant influences on this variable, while at the initial harvest the LSD test disclosed that the weights in the DG and WDG soils fertilized with N, with that in the former numerically the greatest overall but differing only marginally from the one found in the latter, were both distinguishable from the weights in unfertilized WDG and the AD soils regardless of fertility treatment. Furthermore, total seedling weight in DG soil with P added also significantly exceeded those in AD soil without exception, while weights in WDG amended with either P or N+P exceeded the ones in unfertilized AD and that with added N+P. At the second harvest, the weight in the DG soil with N+P was the greatest overall and it exceeded that found in this soil fertilized with N alone, in unfertilized WDG and in that with N+P added, and in all AD treatments, while those in the latter were exceeded by the weights in unfertilized DG and that with P alone and in WDG amended with N or P as well. Additionally, DG fertilized with N and WDG with N+P added produced seedling weights that surpassed that in AD amended with N. Significant disparities detected by the LSD test were especially prevalent at the final harvest, when the greatest weight overall resided in the DG soil fertilized with N+P although it only marginally exceeded that in this soil with N alone added, while both of these were statistically distinct from weights in unfertilized WDG and in all AD treatments, while those in unfertilized DG and in that amended with P and in WDG with either N or N+P added also surpassed the latter. In turn, total weight in WDG fertilized with P exceeded those in all except the P fertility treatment within the AD soil, that in unfertilized WDG exceeded those in AD fertilized with either N or N+P, and the one in AD amended with P exceeded that associated with N+P addition to this soil. The overall influence of soil type on total seedling weight is readily apparent when averages across fertility treatments at the final harvest are compared, as the weight in the AD soil was only 32% of that within DG and 40% of that in WDG.

Shoot/root ratios at the initial harvest in the order of the UF, N, P, and N+P fertility treatments were 1.26, 1.41, 1.14, and 1.40 in the DG soil; 1.48, 1.52, 1.23, and 1.37 in WDG; and 1.23, 1.24, 1.44, and 1.74 within AD. In the same order, those at the second harvest were 0.68, 0.98, 0.68, and 0.88 for DG; 0.90, 1.20, 0.95, and 1.11 for WDG; and 1.05, 1.09, 0.94, and 0.90 for AD. At the final harvest, and in like order, they were 0.68, 0.91, 0.76, and 0.82 in DG; 0.76, 0.91, 0.67, and 0.90 in WDG; and 0.96, 1.07, 1.25, and 1.18 in AD. Significant influences divulged by ANOVA for this variable consisted of the soil type and time of harvest (both $p<0.0001$), fertility treatment ($p=0.0004$), and the soil type × harvest interaction ($p=0.0123$). Initially, and with the AD soil with N+P treatment combination producing the highest overall value, the LSD test distinguished this from the ratios in all other combinations except AD with P added and WDG in combination with either the UF or N fertility treatments. It also distinguished a higher ratio in WDG amended with N from lower ones in both DG and WDG fertilized with P and in AD with N added as well as higher values in unfertilized WDG and in the AD soil fertilized with P from that in the DG soil with added P. Regarding the second harvest, the highest ratio overall was that occurring in WDG fertilized with N, and it differed significantly from all except the N+P fertility treatment within this soil type and from all DG treatments except that entailing added N, while the two exceptions just noted along with the AD treatments in total produced higher ratios than those occurring in the DG soil in combination with the UF and P fertility treatments. At the final harvest, the highest ratio numerically was that associated with the AD soil amended with P, but it differed only marginally from those produced by the N and N+P fertility treatments within this soil type, and values in each of these combinations were denoted by the LSD test to significantly exceed those in DG soil with any except the N fertility treatment along with the ones associated with WDG in combination with either the UF or P treatments. Based on averages across fertility treatments at the final harvest, and in a departure from the pattern regarding all of the variables previously noted, the AD soil induced the highest overall shoot/root ratio of the three types, specifically one 41% greater than that in the DG soil and 38% greater than the one in WDG.

Relationships between shoots and roots

Of the simple linear regression models computed to assess the relationships between shoot and root development in this study, a total of 50 of them specific to measurements at the first harvest proved to be significant, and these overwhelmingly portrayed positive correlations (Table 4). Among them, shoot height, diameter, and weight along with total seedling weight were each positively related to coarse root length and weight, fine root length and weight, total root length and weight, short root count in the coarse and fine fractions plus the colonized short root count in the former, and total short root count, while total shoot weight and that of the seedlings overall were each related to the colonized short root count in the fine fraction and that for the total root systems in additional positive relationships. Negative correlations at the first harvest all entailed shoot/root ratio as the dependent variable which was related to fine and total root length and weight along with the fine fraction and total short root counts. The proportion of the variation in the dependent variables explained by that in the independent variables varied widely within the models based on the initial measurements, spanning a range of from less than 10% to more

Independent variable	Dependent variable	Correlation	F-test p-value	Model r^2
Harvest #1:				
Coarse root length	Shoot height	Positive	<0.0001	0.6027
Coarse root length	Shoot diameter	Positive	<0.0001	0.5942
Coarse root length	Total shoot weight	Positive	<0.0001	0.772
Coarse root length	Total seedling weight	Positive	<0.0001	0.8144
Fine root length	Shoot height	Positive	<0.0001	0.5117
Fine root length	Shoot diameter	Positive	<0.0001	0.3654
Fine root length	Total shoot weight	Positive	<0.0001	0.6106
Fine root length	Total seedling weight	Positive	<0.0001	0.6841
Fine root length	Shoot/root ratio	Negative	0.0118	0.1045
Total root length	Shoot height	Positive	<0.0001	0.5168
Total root length	Shoot diameter	Positive	<0.0001	0.3711
Total root length	Total shoot weight	Positive	<0.0001	0.6173
Total root length	Total seedling weight	Positive	<0.0001	0.691
Total root length	Shoot/root ratio	Negative	0.0119	0.1041
Coarse root weight	Shoot height	Positive	<0.0001	0.5794
Coarse root weight	Shoot diameter	Positive	<0.0001	0.6029
Coarse root weight	Total shoot weight	Positive	<0.0001	0.802
Coarse root weight	Total seedling weight	Positive	<0.0001	0.834
Fine root weight	Shoot height	Positive	<0.0001	0.5717
Fine root weight	Shoot diameter	Positive	<0.0001	0.5229
Fine root weight	Total shoot weight	Positive	<0.0001	0.8179
Fine root weight	Total seedling weight	Positive	<0.0001	0.918
Fine root weight	Shoot/root ratio	Negative	0.0062	0.1222
Total root weight	Shoot height	Positive	<0.0001	0.611
Total root weight	Shoot diameter	Positive	<0.0001	0.5769
Total root weight	Total shoot weight	Positive	<0.0001	0.8671
Total root weight	Total seedling weight	Positive	<0.0001	0.956
Total root weight	Shoot/root ratio	Negative	0.014	0.0996
Coarse fraction short root #	Shoot height	Positive	<0.0001	0.3807
Coarse fraction short root #	Shoot diameter	Positive	<0.0001	0.3502
Coarse fraction short root #	Total shoot weight	Positive	<0.0001	0.4822
Coarse fraction short root #	Total seedling weight	Positive	<0.0001	0.4874
Coarse fraction colonized short root #	Shoot height	Positive	0.0004	0.1937
Coarse fraction colonized short root #	Shoot diameter	Positive	0.0061	0.1227
Coarse fraction colonized short root #	Total shoot weight	Positive	0.0002	0.2172
Coarse fraction colonized short root #	Total seedling weight	Positive	0.0001	0.2238
Fine fraction short root #	Shoot height	Positive	<0.0001	0.4193
Fine fraction short root #	Shoot diameter	Positive	<0.0001	0.2766
Fine fraction short root #	Total shoot weight	Positive	<0.0001	0.5594
Fine fraction short root #	Total seedling weight	Positive	<0.0001	0.6386
Fine fraction short root #	Shoot/root ratio	Negative	0.0191	0.091
Fine fraction colonized short root #	Total shoot weight	Positive	0.0101	0.1087
Fine fraction colonized short root #	Total seedling weight	Positive	0.003	0.1417
Total short root #	Shoot height	Positive	<0.0001	0.4236
Total short root #	Shoot diameter	Positive	<0.0001	0.2807
Total short root #	Total shoot weight	Positive	<0.0001	0.5648
Total short root #	Total seedling weight	Positive	<0.0001	0.6439
Total short root #	Shoot/root ratio	Negative	0.0195	0.0905
Total colonized short root #	Total shoot weight	Positive	0.009	0.1118
Total colonized short root #	Total seedling weight	Positive	0.0027	0.1452
Harvest # 2:				
Coarse root length	Shoot height	Positive	<0.0001	0.4276
Coarse root length	Shoot diameter	Positive	<0.0001	0.5904
Coarse root length	Stem weight	Positive	<0.0001	0.495
Coarse root length	Foliage weight	Positive	<0.0001	0.4982
Coarse root length	Foliage weight %	Negative	0.0003	0.2033
Coarse root length	Total shoot weight	Positive	<0.0001	0.5233
Coarse root length	Total seedling weight	Positive	<0.0001	0.6042
Coarse root length	Shoot/root ratio	Negative	0.0202	0.0897

Fine root length	Shoot height	Positive	<0.0001	0.5844
Fine root length	Shoot diameter	Positive	<0.0001	0.6859
Fine root length	Stem weight	Positive	<0.0001	0.7299
Fine root length	Foliage weight	Positive	<0.0001	0.6787
Fine root length	Foliage weight %	Negative	<0.0001	0.2845
Fine root length	Total shoot weight	Positive	<0.0001	0.7251
Fine root length	Total seedling weight	Positive	<0.0001	0.8159
Fine root length	Shoot/root ratio	Negative	0.0052	0.1276
Total root length	Shoot height	Positive	<0.0001	0.586
Total root length	Shoot diameter	Positive	<0.0001	0.6888
Total root length	Stem weight	Positive	<0.0001	0.7315
Total root length	Foliage weight	Positive	<0.0001	0.6807
Total root length	Foliage weight %	Negative	<0.0001	0.2853
Total root length	Total shoot weight	Positive	<0.0001	0.727
Total root length	Total seedling weight	Positive	<0.0001	0.8183
Total root length	Shoot/root ratio	Negative	0.005	0.1279
Coarse root weight	Shoot height	Positive	<0.0001	0.597
Coarse root weight	Shoot diameter	Positive	<0.0001	0.7568
Coarse root weight	Stem weight	Positive	<0.0001	0.7274
Coarse root weight	Foliage weight	Positive	<0.0001	0.6728
Coarse root weight	Foliage weight %	Negative	<0.0001	0.2721
Coarse root weight	Total shoot weight	Positive	<0.0001	0.7214
Coarse root weight	Total seedling weight	Positive	<0.0001	0.8289
Coarse root weight	Shoot/root ratio	Negative	0.0085	0.1134
Fine root weight	Shoot height	Positive	<0.0001	0.6623
Fine root weight	Shoot diameter	Positive	<0.0001	0.656
Fine root weight	Stem weight	Positive	<0.0001	0.6952
Fine root weight	Foliage weight	Positive	<0.0001	0.6009
Fine root weight	Foliage weight %	Negative	<0.0001	0.4826
Fine root weight	Total shoot weight	Positive	<0.0001	0.6585
Fine root weight	Total seedling weight	Positive	<0.0001	0.904
Fine root weight	Shoot/root ratio	Negative	<0.0001	0.3055
Total root weight	Shoot height	Positive	<0.0001	0.6832
Total root weight	Shoot diameter	Positive	<0.0001	0.7097
Total root weight	Stem weight	Positive	<0.0001	0.7376
Total root weight	Foliage weight	Positive	<0.0001	0.6461
Total root weight	Foliage weight %	Negative	<0.0001	0.4604
Total root weight	Total shoot weight	Positive	<0.0001	0.7051
Total root weight	Total seedling weight	Positive	<0.0001	0.9355
Total root weight	Shoot/root ratio	Negative	<0.0001	0.2752
Coarse fraction short root #	Shoot height	Positive	<0.0001	0.2468
Coarse fraction short root #	Shoot diameter	Positive	<0.0001	0.3276
Coarse fraction short root #	Stem weight	Positive	<0.0001	0.2965
Coarse fraction short root #	Foliage weight	Positive	0.0002	0.2113
Coarse fraction short root #	Foliage weight %	Negative	0.0044	0.1316
Coarse fraction short root #	Total shoot weight	Positive	<0.0001	0.2493
Coarse fraction short root #	Total seedling weight	Positive	<0.0001	0.335
Coarse fraction colonized short root #	Shoot height	Positive	0.0046	0.13
Coarse fraction colonized short root #	Shoot diameter	Positive	0.0056	0.1248
Coarse fraction colonized short root #	Stem weight	Positive	0.0017	0.1577
Coarse fraction colonized short root #	Foliage weight	Positive	0.0008	0.1761
Coarse fraction colonized short root #	Total shoot weight	Positive	0.0009	0.1751
Coarse fraction colonized short root #	Total seedling weight	Positive	0.0011	0.1684
Fine fraction short root #	Shoot height	Positive	<0.0001	0.5472
Fine fraction short root #	Shoot diameter	Positive	<0.0001	0.5202
Fine fraction short root #	Stem weight	Positive	<0.0001	0.6234
Fine fraction short root #	Foliage weight	Positive	<0.0001	0.6037
Fine fraction short root #	Foliage weight %	Negative	<0.0001	0.3226
Fine fraction short root #	Total shoot weight	Positive	<0.0001	0.6348
Fine fraction short root #	Total seedling weight	Positive	<0.0001	0.762
Fine fraction short root #	Shoot/root ratio	Negative	0.0013	0.1653

Fine fraction colonized short root #	Shoot height	Positive	<0.0001	0.3748
Fine fraction colonized short root #	Shoot diameter	Positive	<0.0001	0.3109
Fine fraction colonized short root #	Stem weight	Positive	<0.0001	0.3242
Fine fraction colonized short root #	Foliage weight	Positive	<0.0001	0.3025
Fine fraction colonized short root #	Foliage weight %	Negative	<0.0001	0.3656
Fine fraction colonized short root #	Total shoot weight	Positive	<0.0001	0.3208
Fine fraction colonized short root #	Total seedling weight	Positive	<0.0001	0.5029
Fine fraction colonized short root #	Shoot/root ratio	Negative	<0.0001	0.2716
Total short root #	Shoot height	Positive	<0.0001	0.5499
Total short root #	Shoot diameter	Positive	<0.0001	0.5239
Total short root #	Stem weight	Positive	<0.0001	0.6267
Total short root #	Foliage weight	Positive	<0.0001	0.6059
Total short root #	Foliage weight %	Negative	<0.0001	0.3241
Total short root #	Total shoot weight	Positive	<0.0001	0.6375
Total short root #	Total seedling weight	Positive	<0.0001	0.7657
Total short root #	Shoot/root ratio	Negative	0.0012	0.1658
Total colonized short root #	Shoot height	Positive	<0.0001	0.376
Total colonized short root #	Shoot diameter	Positive	<0.0001	0.3122
Total colonized short root #	Stem weight	Positive	<0.0001	0.3259
Total colonized short root #	Foliage weight	Positive	<0.0001	0.3044
Total colonized short root #	Foliage weight %	Negative	<0.0001	0.3641
Total colonized short root #	Total shoot weight	Positive	<0.0001	0.3227
Total colonized short root #	Total seedling weight	Positive	<0.0001	0.5044
Total colonized short root #	Shoot/root ratio	Negative	<0.0001	0.2696
Harvest #3				
Coarse root length	Shoot height	Positive	<0.0001	0.4889
Coarse root length	Shoot diameter	Positive	<0.0001	0.5841
Coarse root length	Stem weight	Positive	<0.0001	0.5013
Coarse root length	Foliage weight	Positive	<0.0001	0.5126
Coarse root length	Foliage weight %	Negative	0.0239	0.0849
Coarse root length	Total shoot weight	Positive	<0.0001	0.5517
Coarse root length	Total seedling weight	Positive	<0.0001	0.6525
Coarse root length	Shoot/root ratio	Negative	0.0007	0.1798
Fine root length	Shoot height	Positive	<0.0001	0.5381
Fine root length	Shoot diameter	Positive	<0.0001	0.6404
Fine root length	Stem weight	Positive	<0.0001	0.6559
Fine root length	Foliage weight	Positive	<0.0001	0.4752
Fine root length	Foliage weight %	Negative	<0.0001	0.2451
Fine root length	Total shoot weight	Positive	<0.0001	0.581
Fine root length	Total seedling weight	Positive	<0.0001	0.8093
Fine root length	Shoot/root ratio	Negative	<0.0001	0.3226
Total root length	Shoot height	Positive	<0.0001	0.5394
Total root length	Shoot diameter	Positive	<0.0001	0.6419
Total root length	Stem weight	Positive	<0.0001	0.6568
Total root length	Foliage weight	Positive	<0.0001	0.4769
Total root length	Foliage weight %	Negative	<0.0001	0.2446
Total root length	Total shoot weight	Positive	<0.0001	0.5826
Total root length	Total seedling weight	Positive	<0.0001	0.8107
Total root length	Shoot/root ratio	Negative	<0.0001	0.3225
Coarse root weight	Shoot height	Positive	<0.0001	0.673
Coarse root weight	Shoot diameter	Positive	<0.0001	0.8049
Coarse root weight	Stem weight	Positive	<0.0001	0.8079
Coarse root weight	Foliage weight	Positive	<0.0001	0.6961
Coarse root weight	Foliage weight %	Negative	0.004	0.1342
Coarse root weight	Total shoot weight	Positive	<0.0001	0.7968
Coarse root weight	Total seedling weight	Positive	<0.0001	0.9139
Coarse root weight	Shoot/root ratio	Negative	0.0007	0.1825
Fine root weight	Shoot height	Positive	<0.0001	0.554
Fine root weight	Shoot diameter	Positive	<0.0001	0.6796
Fine root weight	Stem weight	Positive	<0.0001	0.6964

Fine root weight	Foliage weight	Positive	<0.0001	0.4893
Fine root weight	Foliage weight %	Negative	<0.0001	0.3182
Fine root weight	Total shoot weight	Positive	<0.0001	0.6055
Fine root weight	Total seedling weight	Positive	<0.0001	0.8947
Fine root weight	Shoot/root ratio	Negative	<0.0001	0.3915
Total root weight	Shoot height	Positive	<0.0001	0.5915
Total root weight	Shoot diameter	Positive	<0.0001	0.7223
Total root weight	Stem weight	Positive	<0.0001	0.7374
Total root weight	Foliage weight	Positive	<0.0001	0.5384
Total root weight	Foliage weight %	Negative	<0.0001	0.2903
Total root weight	Total shoot weight	Positive	<0.0001	0.6563
Total root weight	Total seedling weight	Positive	<0.0001	0.9264
Total root weight	Shoot/root ratio	Negative	<0.0001	0.3616
Coarse fraction short root #	Shoot height	Positive	<0.0001	0.2845
Coarse fraction short root #	Shoot diameter	Positive	<0.0001	0.3494
Coarse fraction short root #	Stem weight	Positive	<0.0001	0.3531
Coarse fraction short root #	Foliage weight	Positive	<0.0001	0.4157
Coarse fraction short root #	Total shoot weight	Positive	<0.0001	0.4264
Coarse fraction short root #	Total seedling weight	Positive	<0.0001	0.4332
Coarse fraction colonized short root #	Shoot height	Positive	0.0002	0.2136
Coarse fraction colonized short root #	Shoot diameter	Positive	0.0002	0.2137
Coarse fraction colonized short root #	Stem weight	Positive	<0.0001	0.2805
Coarse fraction colonized short root #	Foliage weight	Positive	0.0002	0.2105
Coarse fraction colonized short root #	Total shoot weight	Positive	<0.0001	0.2539
Coarse fraction colonized short root #	Total seedling weight	Positive	<0.0001	0.2508
Fine fraction short root #	Shoot height	Positive	<0.0001	0.5953
Fine fraction short root #	Shoot diameter	Positive	<0.0001	0.6679
Fine fraction short root #	Stem weight	Positive	<0.0001	0.6437
Fine fraction short root #	Foliage weight	Positive	<0.0001	0.4417
Fine fraction short root #	Foliage weight %	Negative	<0.0001	0.2775
Fine fraction short root #	Total shoot weight	Positive	<0.0001	0.5518
Fine fraction short root #	Total seedling weight	Positive	<0.0001	0.7878
Fine fraction short root #	Shoot/root ratio	Negative	<0.0001	0.3487
Fine fraction colonized short root #	Shoot height	Positive	<0.0001	0.4898
Fine fraction colonized short root #	Shoot diameter	Positive	<0.0001	0.4076
Fine fraction colonized short root #	Stem weight	Positive	<0.0001	0.3627
Fine fraction colonized short root #	Foliage weight	Positive	<0.0001	0.2935
Fine fraction colonized short root #	Foliage weight %	Negative	0.0016	0.1584
Fine fraction colonized short root #	Total shoot weight	Positive	<0.0001	0.344
Fine fraction colonized short root #	Total seedling weight	Positive	<0.0001	0.4724
Fine fraction colonized short root #	Shoot/root ratio	Negative	<0.0001	0.237
Total short root #	Shoot height	Positive	<0.0001	0.5971
Total short root #	Shoot diameter	Positive	<0.0001	0.6702
Total short root #	Stem weight	Positive	<0.0001	0.6461
Total short root #	Foliage weight	Positive	<0.0001	0.4447
Total short root #	Foliage weight %	Negative	<0.0001	0.2765
Total short root #	Total shoot weight	Positive	<0.0001	0.5548
Total short root #	Total seedling weight	Positive	<0.0001	0.7906
Total short root #	Shoot/root ratio	Negative	<0.0001	0.348
Total colonized short root #	Shoot height	Positive	<0.0001	0.493
Total colonized short root #	Shoot diameter	Positive	<0.0001	0.4107
Total colonized short root #	Stem weight	Positive	<0.0001	0.3665
Total colonized short root #	Foliage weight	Positive	<0.0001	0.2965
Total colonized short root #	Foliage weight %	Negative	0.0016	0.1585
Total colonized short root #	Total shoot weight	Positive	<0.0001	0.3475
Total colonized short root #	Total seedling weight	Positive	<0.0001	0.4761
Total colonized short root #	Shoot/root ratio	Negative	<0.0001	0.2369

Table 4: Significant simple linear regression models relating shoot development of ponderosa pine seedlings to that of the root systems as influenced by soil type and fertilization [1]. Models are based on 60 or fewer observations (n ≤ 60) depending on the number of seedlings from which the pertinent values could be derived.

than 90%. Generally, models featuring root lengths and weights as the independent components were among the strongest followed by those incorporating short root counts while the ones involving colonized short root counts were weakest, but any model featuring shoot/root ratio as the dependent variable was exceedingly weak regardless of its independent counterpart.

A total of 93 significant models were generated from measurements at the second harvest, with positive correlations again predominant (Table 4). Of these, shoot height, diameter, and total weight, stem and foliage weight, and total seedling weight were each positively related to coarse, fine, and total root length and weight, coarse and fine fraction short root count along with that for the total root system, and colonized short root count within the coarse and fine fractions plus the total system count. As for negative correlations, foliage weight percentage was thus related to each of the independent variables just noted except the colonized short root count within the coarse fraction while shoot/root ratio was negatively related to each of them except the short root and colonized short root count within this fraction. The variation in the dependent variables accounted for by that in their independent counterparts in the models based on second harvest measurements again varied from less than 10% to more than 90%. Overall, models with root lengths and weights as the independent components were among the strongest along with those featuring fine fraction and total short root count while among consistently weak ones were models incorporating coarse fraction short root count, but weaker still were those involving colonized short root count within the latter fraction plus some of the models with either shoot/root ratio or foliage weight percentage as the dependent variable.

With positive relationships continuing to predominate, a total of 92 significant models were computed based on measurements at the final harvest (Table 4). Duplicating verbatim the positive correlations denoted above specific to the second harvest, shoot height, diameter, and total weight, stem and foliage weight, and total seedling weight were thus related to coarse, fine, and total root length and weight, coarse and fine fraction short root count as well as that for the total root system, and colonized short root count within the coarse and fine fractions plus the total system count at the final harvest. Regarding negative relationships, foliage weight percentage and shoot/root ratio were thus correlated with each of the independent variables just noted except the short root and colonized short root count within the coarse fraction. As had proven true at the first two harvests, variation in the dependent variables accounted for by that in the independent ones again varied from less than 10% to more than 90%. And, again, models with root lengths and weights along with those featuring fine fraction and total short root count as the independent components were generally among the strongest while the weakest ones included those incorporating the coarse fraction colonized short root count plus some with shoot/root ratio or foliage weight percentage as the dependent variable.

Discussion

Paramount among the influences exerted on seedling shoot development in this study was the soil type, with the andesitic properties embodied in the AD soil proving to be a poor medium for promoting the growth of above-ground tissues in ponderosa pine. This was readily evident in the height and diameter dimension measurements as well as the dry weight measurements at each of the three junctures of the study when such growth measures were assessed. Comparatively, the soils derived from decomposed granite proved to be favorable to shoot development, especially that designated as DG here with the more weathered WDG nearly its equal, and the disparities between these and the AD soil were pronounced to such extent that total shoot weight of seedlings grown in the latter was less than one-half of that produced in either the DG or WDG soils at the conclusion of the study. Furthermore, and perhaps even more critical at the seedling stage of development, foliage weight in the AD soil was at most one-half of that produced in the granitic ones at the final harvest. Although beyond the scope of the present investigation, it is probable that the muted growth stimulation provided by the AD soil, given that all seedlings were subjected to an irrigation regime intended to largely eliminate moisture stress as a limiting factor, reflects a nutritional limitation that may involve the proclivity of andesitic soils to fix phosphorus [27,28], the solubility and therefore plant availability of which is controlled by iron oxides and aluminum sesquioxides at the pH of most forest soils [29]. Nevertheless, the capacity of the nutrient additions employed here to enhance shoot growth did not entail an effect nearly as pronounced as that of soil type, and to the extent discernible was most prevalent within the DG soil, as significant differences among fertility treatments in the AD soil occurred only in measurements from the final harvest, specifically in stem diameter, foliage weight, and total shoot weight, and although in each instance P fertilization produced the highest value, the addition of N+P produced the lowest one by a considerable margin in what may have constituted an antagonistic interaction between the two nutrients in this soil. Regardless, when occurring in the DG and WDG soils such differences, which were confined to the first two harvests for the former and to the initial one only for the latter, usually provided evidence of a favorable response to either N or N+P fertilization. Growth stimulation by N amendments in forestry applications has generally been accredited to their enlargement of leaf area and therefore photosynthetic surface area [30], while that by P is undoubtedly related to the multiple energy compounds of which this element is an indispensable component [31]. Previous studies of similar duration using the same seed lot as that here but planted in a soil mix differing substantially from any of the three soil types used in the present investigation have revealed prolonged positive shoot growth responses to N fertilization while those to added P have been ephemeral [32-34].

Based on the rudimentary measures of length and weight, the incapacity of the AD soil to promote seedling growth equal to that of the DG and WDG soils was as obvious in root growth as it was in that of the shoots. For root length, that in the AD soil specific to the coarse fraction was approximately one-half of the length produced in DG and less than two-thirds of that in WDG at the final harvest, while fine and total root length in the former were one-third of those in DG and less than one-half of the ones in WDG. Similarly, final root weights divided into coarse and fine fractions plus their total in the AD soil were all less than one-third of those in DG and only marginally exceeded one-third of the ones in WDG. Seemingly apparent here is the interrelationship between the limited capacity of a diminished root system to supply the mineral nutrition needed to promote shoot growth, and in turn the limited capacity of constricted foliar development to generate the photosynthates needed to energize root growth, both of which may be attributable to the aforementioned dearth of plant-available phosphorus. Regardless of the actual causation, however, the coupling of comparatively small root systems with near equally small shoots ultimately yielded total seedling weights in the AD soil type that were approximately one-third of that in the DG soil and considerably less than one-half of that in WDG. In another parallel with shoot development, the influence of fertility treatment on root length and weight was much subdued relative to that of soil type, and when significant differences were revealed within the AD soil, which were

mostly confined to root length at the final harvest although with coarse fraction weight then as an additional instance, P fertilization again produced the highest value but that with N+P produced the lowest one by a substantial margin. Furthermore, significant disparities in the other two soil types were again confined to the first two harvests and positive responses to nutrient additions were sporadic with little consistency across variables to any such treatment in particular. The previous studies with ponderosa pine seedlings cited above in regards to shoot responses to fertilization also documented root lengths and weights that reflected a more pronounced and persistent stimulation by N fertilization than that by P [32-34].

Another aspect of root system development examined in this study, and another one clearly impacted by soil type, was the proliferation of short roots. Irrespective of their status regarding mycorrhizal infection, the quantification of such at the final harvest revealed that their abundance in the AD soil, with one exception, was either slightly over or somewhat less than one-third of the number found on seedlings grown in the DG and WDG soils whether borne on the coarse or fine fractions or in total. The lone exception was the count specific to the coarse fraction, which in the former was about two-thirds of that in WDG, but the functional contribution of the counts in this fraction in general is questionable because their numbers were minuscule compared to those found on fine roots. Nevertheless, the stark differences in short root abundance between the andesitic and granitic soils were undoubtedly a reflection in part of the limited elongation overall of the root systems in the former, and given their vital role in nutrient absorption by conifers, as reflected in their often being referred to as feeder roots [35], this is further evidence of the generally poor root system development fostered by this soil. Lack of any significant differences among fertility treatments within the AD soil at any juncture of the study clearly infers that fertilization was of no discernible consequence in rectifying this deficiency, and its influence on short root proliferation within the DG and WDG soils, as manifested in significant disparities among mean values therein, was confined to the counts at the first two harvests with perhaps the clearest among vague indications of a beneficial nutrient augmentation effect consisting of one for P added to the DG soil in the initial fine fraction and total counts.

Closely aligned with short roots functionally are mycorrhizae, and closely aligned with the short root counts in this study were the colonized short root counts, as the responses to soil type of the latter closely paralleled those of the former to such extent that even the magnitude of the disparities between the andesitic and granitic soils at the final harvest differed only marginally. Also, the tepid responses to fertility treatment noted above for overall count largely extended to colonized count, with the most apparent favorable reaction to nutrient augmentation again likely that to P in the initial fine fraction and total counts within the DG soil, while all differences among means within the AD soil type were nonsignificant for the entirety of the study. Expressing the colonized count as a percentage of the overall count produced somewhat of a shift in the responses to soil type in that no effect was discerned for the coarse fraction at all while identical fine fraction and total root system percentages at the final harvest for seedlings that had been grown in the WDG and AD soils contrasted against a higher one in each case for those grown in DG. Regarding fertility treatment effects on colonization percentages, significant differences among means within soil types included cases in which P fertilization was associated with higher values, such as those specific to both the fine fraction and total system in the DG soil at the first harvest and in the AD soil at the second one, and alternatively with lower values, such as those specific to the same but in WDG at the former. Furthermore, fertilization with N and with N+P depressed these percentages in WDG at the second and third harvests, respectively. Elevated substrate fertility has often been assumed to suppress ectomycorrhizal colonization in conifer seedlings [36] although responses in western USA species to higher fertilization regimes in forest nurseries have been somewhat mixed with positive, negative, and inconsequential outcomes [37-40] and inconsistencies here in both the infected short root count and resulting percentage did not provide much assurance for any generalization regarding this specific host and symbiont combination. Previous studies that have examined this topic in conifer nurseries have largely involved induced colonization using pure culture inoculation with select symbionts while the origin of the mycorrhizae here were spores and hyphae contained in the soils at their collection probably augmented with additional wind borne spores deposited into the seedling containers from pine stands near the greenhouse, a comparatively indiscriminate source of infection that may have confounded the relationship between fertility and mycorrhization.

Although root system development was the primary focus of this investigation, quantification of selected shoot growth parameters permitted an examination of the relationships between above-ground and below-ground development during the seedling stage and in particular a comparison of the potency of various root variables regarding their influence on shoot growth. That the basic shoot growth measures used here entailing dimensions and dry weight were positively related to the common root system measures of length and weight, and that these were among the strongest correlations computed throughout the study, was unsurprising given the essential physical and physiological support provided by root systems to aerial plant tissues. Overall, there was little clear distinction between root lengths and weights in the strength of these models. However, a variable derived from dry weights, namely shoot/root ratio which is a commonly monitored indicator of planting stock quality in conifer nurseries [41,42], was negatively related to root weights along with the other basic below-ground growth measures, as would be expected, but these regression models were generally among the weakest ones computed, suggesting that shoot mass was somewhat more of a driver in this variable than that of the roots. On a related note, other negative relationships disclosed by this study entailed such between foliage weight expressed as a percentage of total seedling weight and root biomass plus associated lengths as revealed at the second and third harvests, which while also tending to be among the weaker of the significant models suggest that larger root systems came at the expense of foliar development. Returning to positive relationships, a substantial number of them featured overall short root abundance and colonized short root counts as the independent variables with which shoot measures were correlated, as would be expected given the vital role of short roots in conifer nutrition and in particular their serving as the loci for most ectomycorrhizal infections in such species [43], with the latter of such nutritional importance that they constitute obligate symbioses in certain genera including the pines [44]. Significant models involving overall count and colonized count were approximately equal in number, but those specific to the coarse fraction, and most especially among them ones involving colonized count, were among the weaker models computed in the study, perhaps reflecting the functional transition from one primarily of nutrient and water uptake to conductance and storage as tree roots thicken with age [31]. Regardless, probably the most glaring omission among the significant models generated in this study were any relying upon the percentage of short roots colonized, a common approach to expressing ectomycorrhizal infection levels, as the independent variable even

when calculated specifically for the fine root fraction and regardless of the harvest from which such percentages were derived, which serves to confirm a previous report that although noted the widespread use of this practice also called its propriety into question [20] and contributes to a conclusion that mycorrhization expressed simply as colonized short root quantity per seedling is a better indicator of the influence it exerts on seedling growth.

In summary, this study entailed an examination of the capacity of soil types common in the Sierra Nevada, as altered by nutritional augmentation, to promote seedling development in ponderosa pine, particularly regarding their root systems but including an assessment of the influence its development exerted on shoot growth. Along with that of shoot dimensions and dry weight, soils derived from decomposed granite far surpassed one of andesitic origin in promoting root growth within both the coarse and fine root fractions as quantified through measurements of length and weight at three intervals dispersed over the nearly 10-month duration of the study. Seedlings grown in the granitic soils also had far more short roots and ectomycorrhizae, again irrespective of root size fraction. For both shoots and roots, the magnitude of these responses was somewhat more pronounced in a less weathered than in a more heavily weathered granitic soil. Fertilization at the outset of the study with either N or P or both did little to alleviate the growth deficiencies in the andesitic soil in either above- or below-ground seedling tissues, and its influences in the granitic soils were muted, somewhat erratic, and largely ephemeral. Shoot growth was strongly correlated with root system length and weight and at least moderately so with short root and mycorrhizal counts, although such counts were of greater predictive power when limited to the fine rather the coarse root size fraction, but it was not correlated with ectomycorrhizal infection percentage. These results provide insight into edaphic influences on the early development of one of the most prominent tree species in western USA forests.

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