

Root biomass distribution under three cover types in a patchy *Pseudotsuga menziesii* forest in western Canada

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Abstract – We investigated the relationship between cover type and root biomass distribution and allocation to different root size classes in a naturally regenerated, dry, Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forest in the southern interior of British Columbia, Canada. The site was selectively harvested 32 years previously; residual stems were 30 cm and 130–170 years old at breast height at the time of study. A total of nine pits (each measuring 1.0 m × 1.0 m) were excavated to a depth of 1.0 m under three different cover types: mature timber, grassy (*Calamagrostis rubescens*) openings (canopy gaps), and regeneration clumps. Total (all diameters) live root biomass ranged from 4.7 kg/m² under the mature timber to 1.9 kg/m² under both regeneration clumps and grassy openings. Thin root (0.1 cm < ϕ ≤ 0.5 cm) biomass was similar across all three cover types (0.8 kg/m²). We suggest that the similarity of thin root biomass across the three cover types is indicative of strong root competition at this resource-poor site: there appears to be no below-ground “root gap” corresponding to the canopy opening above the pinegrass-dominated patches.

Calamagrostis rubescens / Douglas-fir / gap / *Pseudotsuga menziesii* / root biomass

Résumé – Distribution de la biomasse racinaire sous trois types de couvert dans une forêt irrégulière de *Pseudotsuga menziesii* du Canada occidental. Nous avons étudié la relation entre le type de couvert et la répartition de la biomasse racinaire entre différentes classes de dimension des racines, dans une forêt sèche régénérée naturellement de Douglas des Montagnes Rocheuses (*Pseudotsuga menziesii* var. *glauca*) située dans la zone intérieure méridionale de la Colombie Britannique au Canada. Cette station avait subi une coupe à la dimension 32 ans auparavant. Les tiges restantes, âgées de 130 à 170 ans, avaient, au moment de l'étude, un diamètre à hauteur d'homme de 30 cm. On a creusé neuf fosses mesurant chacune 1,0 × 1,0 × 1,0 m sous trois types de couvert : peuplement adulte, clairières à graminées (*Calamagrostis rubescens*) et bouquets de régénération. La biomasse racinaire totale (tous diamètres) va de 4,7 kg/m² sous peuplement adulte à 1,9 kg/m² sous les bouquets de régénération et sous clairières à graminées. La biomasse des racines fines (0,1 cm < ϕ ≤ 0,5 cm) était du même ordre sous les trois types de couvert (0,8 kg/m²). Nous suggérons que cette similitude des valeurs de biomasse de racines fines entre les trois types de couvert est l'indice de l'existence d'une forte concurrence entre racines, dans cette station pauvre en ressources. Les ouvertures dans le couvert forestier se traduisent par des clairières à *Calamagrostis* qui ne sont pas des zones sans racines.

Calamagrostis rubescens / Douglas / trouée / *Pseudotsuga menziesii* / biomasse

1. INTRODUCTION

Plant roots, sometimes referred to as the “hidden half” [21], are a major terrestrial sink for carbon [11]. For example, in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands, roots may account for as much as one-fifth of total stand biomass [5, 15], and it has been calculated that fine root turnover represents 33% of global net primary productivity [9]. Furthermore, roots are important organs of competition, and in some ecosystems, below-ground competition for resources may be more important than that above-ground [3].

Root distribution parameters, such as root density or depth profiles, are considered important indicators of below-ground competition [3, 7]. Thus, variation in the distribution of roots across a landscape may provide important information that

helps us to understand better the above-ground abundance and distribution of species. For example, relationships between above-ground canopy gaps and the availability of below-ground growing space (the “root gaps” of Sanford [16, 17]) have been hypothesized but tested in only a few ecosystems [1, 4, 16, 17, 22].

Our study site, characterized by a continental climate with warm summers and cool winters, was located in a dry Douglas-fir forest (Fig. 1) in southern interior British Columbia, Canada. We became interested in the correspondence between canopy openings and the availability of below-ground growing space because of the patchy regeneration pattern of the dominant tree species, Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), following a diameter-limit harvest [20] at our site about thirty years ago. In the original

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Figure 1. The Pothole Creek research site is characterized by mature Douglas-fir residuals from a selective harvest some 30 years earlier (background), grassy openings dominated by pinegrass (foreground), and dense clumps of Douglas-fir regeneration (left edge).

multi-cohort stand, the distribution of trees of different ages and sizes was very irregular. The selective harvest removed most of the sparser patches of large trees and left denser patches of undersize trees. Dense patches of Douglas-fir regeneration subsequently occupied some of the created openings, but not others, which were quickly overtaken by pinegrass (*Calamagrostis rubescens* Buckl.). The canopy opening above the pinegrass persists to this day, but little is known about what is going on below-ground. Therefore, we excavated three pits, each measuring one cubic meter, beneath each of the three main cover types: mature timber, grassy openings, and regeneration clumps. We compared the biomass distribution and allocation to different root size classes under these three cover types.

2. MATERIALS AND METHODS

2.1. Study site

Field work was conducted in July 1998 near Merritt, British Columbia (the westernmost Canadian province), in the north-east corner of the B.C. Ministry of Forests' Pothole Creek research site (49° 55' 22'' N, 120° 27' 37'' W, elevation 1210 m). Pothole Creek is situated within the interior Douglas-fir (IDF) biogeoclimatic zone which dominates the south-central interior of B.C. Across the IDF zone, the mean temperature is below 0 °C for 2–5 months of the year, and above 10 °C for 3–5 months of the year; annual precipitation ranges from 300 to 750 mm, of which up to half falls as snow [13]. Our study site is more properly classified as a dry, cool subzone (dk1) of the IDF [12]; this subzone covers slightly more than half a million ha, or just less than 1% of the forested landbase of the province of B.C.

The site is dominated by Douglas-fir, with occasional *Pinus contorta* Dougl. and hybrid *Picea engelmannii* × *glauca*. Dominant height (the arithmetic mean height of the tallest 100 trees per ha) is 21.4 m. Basal area of a 1 ha mensuration plot at the site is 22.4 m²/ha, with the above-ground biomass of trees greater than 1.3 m in height estimated to be 13.4 kg/m² (C. Bealle Statland and A.D. Richardson, unpublished data). Small trees (≤ 12 cm diameter) account for about 14% of the basal area, and 7% of the above-ground biomass. The major understory species is pinegrass; other understory species include *Shepherdia canadensis* (L.) Nutt., *Arctostaphylos uva-ursi* (L.) Spreng., *Aster conspicuus* Lindl., *Achillea millefolium* L., and *Linnaea borealis* L.

The site is characterized by three different cover types, which can be classified as follows:

(1) mature residual Douglas-fir: The Pothole Creek site was selectively harvested in 1966, and all of the dominant trees presently at the site are residuals that were not harvested. Generally occurring together in small stands, these trees average about 30 cm in diameter and 130–170 years old at breast height. This mature timber is characterized by little or no understory except for some pinegrass;

(2) dense Douglas-fir regeneration clumps: where regeneration has occurred, trees are small (less than 5 m in height, though most are considerably smaller) and up to 60 years old measured at base. The younger trees have regenerated since the logging in 1966, and the older trees were suppressed until the harvest opened up growing space. Stem density is high, at times approaching 20 stems/m². The understory consists largely of Douglas-fir seedlings and some pinegrass; and

(3) grassy openings: these are dominated almost exclusively by pinegrass, and are notable for their absence of trees greater than 1.3 m in height. There has been little or no Douglas-fir regeneration since the harvest in 1966; if there was any suppressed regeneration prior to the harvest, it has since been out-competed by pinegrass. Stumps remaining from the harvest have been slow to decompose and are scattered throughout these canopy gaps.

The cover types are abbreviated as M (mature timber), R (regeneration clumps), and G (grassy openings).

The soils at Pothole are coarse-textured (sandy loams with generally 5–10% gravels and 10–30% cobbles) and poorly developed, and are classified (C. Braybrook, Ministry of Forests Research Branch, Victoria, B.C., unpublished report) as predominantly Orthic melanic brunisols or Eluviated eutric brunisols (FAO equivalent: Eutric Cambisol). These are typical soils for dry forests in B.C. Soils at the site are generally mildly acidic to neutral, with pH ranging from 5.7 to 6.8. In a preliminary study, soil properties did not appear to explain whether harvested areas regenerated as Douglas-fir, or converted to pinegrass (C. Braybrook, unpublished report).

2.2. Hydraulic excavation

We excavated three pits (1 m × 1 m × 1 m = 1 m³) under each of the three cover types (Fig. 2). The use of coring techniques was deemed inappropriate due to the abundance of cobbles and other

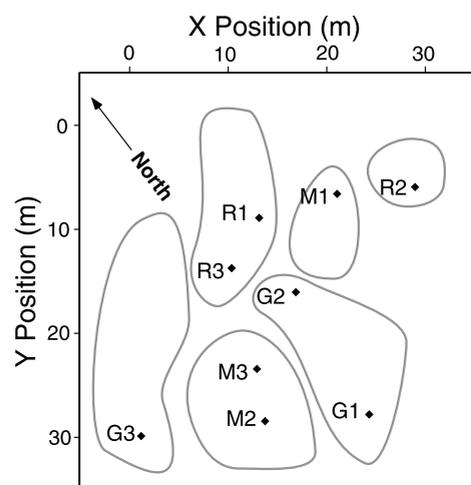


Figure 2. Sketch map of the 0.1 ha corner of the Pothole Creek research site where root excavations were conducted. Lines represent approximate boundaries of the different cover types. Pit locations under each cover type are indicated. Cover types: G, Grassy opening; M, Mature forest; R, Regeneration clump.

coarse fragments in the soil. Pits were located in areas that appeared representative of the appropriate cover type. Pits were hydraulically excavated with a fire pump (Wajax Industries Ltd., Edmonton, Alberta, Canada) powered by an 18 hp engine (Briggs and Stratton Corp., Milwaukee, WI). The choice of hydraulic excavation techniques restricted our excavation area to that which was within reach of the hose, which was limited by the power of the pump and the location and amount of the water supply. Excavation was conducted at water pressures ranging from 350 to 600 kPa. Lower pressures were adequate near the surface, where roots were most abundant and the higher organic matter content resulted in a comparatively soft, loose soil. Higher pressures (up to 1100 kPa) were generally required with increasing depth, as the root density decreased and the difficulty of excavation increased due to hard, cemented soil peds. The highest pressures damaged or broke some roots of $\phi \leq 0.5$ cm (ϕ is mean root diameter) but larger diameter roots generally remained intact; we do not have any estimates available of the amount of biomass thus lost, but we did not observe significant quantities of roots being carried away in the hydraulic runoff.

In each pit, roots were collected and sorted into different size classes based on mean root diameter. We used a modified system based on the classification of Köstler et al. (1968) [10]: thin roots (“Schwachwurzeln”, $0.1 \text{ cm} < \phi \leq 0.5 \text{ cm}$), medium roots (“Grobwurzeln”, $0.5 \text{ cm} < \phi \leq 2.0 \text{ cm}$), large roots (“Derbwurzeln”, $2.0 \text{ cm} < \phi \leq 5.0 \text{ cm}$), and very large roots (“Starkwurzeln”, $\phi > 5.0 \text{ cm}$). We did not attempt to further subdivide thin roots or separate fine and very fine roots; the thin root category thus includes fine roots. Dead and decaying roots with $\phi > 0.5 \text{ cm}$ were collected but not sorted by size class. No attempt was made to separate roots by species.

Preliminary excavations indicated that the majority of the fine and thin root mat was contained in the upper 20 cm soil horizon, and so to differentiate surface roots from those occurring at deeper depths, roots from the 0–20 cm and 20–100 cm horizons were separated. Following excavation, roots were oven-dried at 70 °C to constant weight.

2.3. Pit descriptions

Within 1 m of the edge of the pits under M, there were, on average, 2.7 mature Douglas-fir trees, with a mean diameter at breast height (DBH) of 26.4 cm. Within 1 m of the edge of the pits under R, there

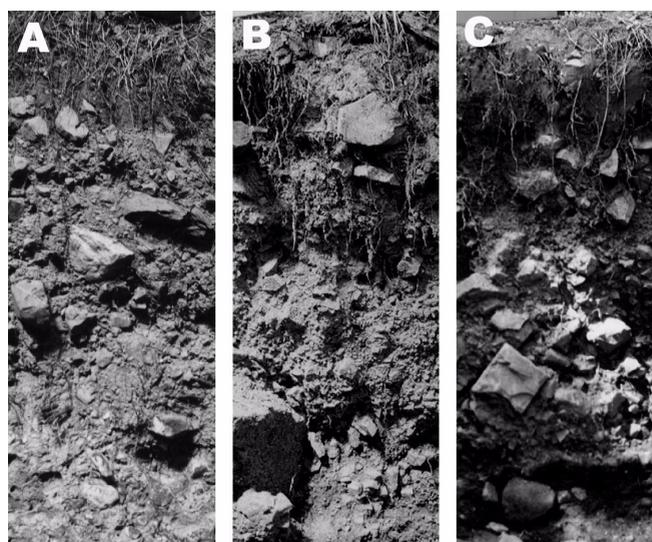


Figure 3. Sample soil profiles for one plot from each cover type. (A) Grassy openings, plot G3; (B) Mature forest, plot M3; (C) Regeneration clump, plot R3.

were, on average, 18.3 small (less than 5 m in height, but generally much smaller) Douglas-fir stems. For pit G1, the nearest Douglas-fir (25.6 cm DBH) was 6 m from the pit edge. For pit G2, the nearest Douglas-fir (23.8 cm DBH) was 3 m from the pit edge. For pit G3, there was a large, dense clump of old but quite small (≈ 5 –10 cm DBH) Douglas-fir about 5 m from the edge of the pit.

A basic description of the soil profile in each pit is given in Table I. The abundance and size of coarse fragments varied with depth and also among pits; coarse fragments were generally rare in the upper 20 cm horizon, which was the approximate depth of organic matter accumulation and also the zone of densest rooting. Two types of coarse fragments were common: angular, blocky fragments resembling shattered bedrock, and rounded cobbles more typical of glacial till. Sample pit profiles are illustrated in Figure 3 for each cover type.

2.4. Statistical analysis

To test for differences in root biomass among different cover types, we used a Monte Carlo type procedure (often referred to as a “randomization test”) described by Schabenberger and Pierce (2001) [19]. For each root diameter class, contrasts were constructed to compare the mean biomass under each cover type against the mean of the other two cover types combined. The significance of contrasts is reported at two different levels, $\alpha = 0.05$ and $\alpha = 0.10$; the higher α is accepted in some cases to reduce the likelihood of a Type II error. The former was chosen because it has become the “gold standard” for good or ill; the latter to increase the power of these tests [6].

3. RESULTS

3.1. Biomass by root size classes

On average, there was more total (live + dead) root biomass beneath M (mature timber, $5.4 \pm 1.5 \text{ kg/m}^2$, mean \pm 1 S.D.) than R (regeneration clumps), and less under G (grassy openings, $3.8 \pm 1.0 \text{ kg/m}^2$) (Fig. 4a; contrast between M and G, R significant at $P \leq 0.10$). Considering only live roots, however, root biomass was nearly identical ($\approx 2 \text{ kg/m}^2$) for G and R, whilst beneath M there was more than double that ($4.6 \pm 1.6 \text{ kg/m}^2$,

Table I. Brief descriptions of soils in root excavation pits, grouped by cover type.

Pit #	Depth	Description
Mature clumps		
M1	0–20 cm	high OM, few CF, abundant roots of all size classes
	20+ cm	hard sand-silt, some large CF, few roots
M2	0–15 cm	few CF, many roots of all size classes
	15–50 cm	many CF, hard sand-silt, few roots
	50+ cm	abundant CF, very hard sand-silt, some large roots to depth of 1.0 m
M3	0–20 cm	high OM, few CF, soft sandy loam with many roots
	20–40 cm	some CF, few roots, hard sandy loam
	40–60 cm	many small CF, very hard sand-silt
	60+ cm	coarse sand, angular CF of all sizes
Regeneration patches		
R1	0–15 cm	dark horizon with high OM, few CF, abundant roots
	15–90 cm	hard, compact horizon, mostly sand and silt, many small CF, some large CF
	90+ cm	abundant roots spread out across impermeable layer of silt-clay
R2	0–20 cm	dark horizon with high OM, few CF, abundant roots
	20–50 cm	silt-sand horizon, some coarse sand, few small CF, large CF common, few roots
	50+ cm	hard, sandy horizon with few roots
R3	0–20 cm	dark, soft horizon with many roots
	20–50 cm	gravelly sand, many CF, few roots
	50–100 cm	hard, coarse sand with some gravel, abundant large and angular CF, and few roots
	100+ cm	dense but thin layer of roots across top of impermeable silt-clay horizon embedded with rounded cobbles
Grassy openings		
G1	0–100 cm	few CF, all small, soft sand-silt with many roots across entire profile
	100+ cm	dense but thin layer of roots across top of impermeable silt-clay embedded with some larger CF
G2	0–10 cm	sandy horizon, some OM, abundant roots
	10–40 cm	hard layer of sand-silt, some CF
	40–80 cm	very hard, many angular CF to depth of 60 cm, few CF below 60 cm
	80+ cm	dense but thin layer of roots across top of impermeable silt-clay
G3	0–30 cm	abundant roots in dark horizon with few CF
	30–70 cm	very hard horizon of gravelly, coarse sand, many large CF, some fine roots
	70–100 cm	some small CF, occasional fine roots
	100+ cm	dense but thin layer of roots across top of impermeable silt-clay

Note: pit numbers correspond to those in Figure 2. Abbreviations: OM, organic matter; CF, coarse fragments (small: ≤ 5 cm; large: > 5 cm).

Fig. 4b; contrast M vs. G, R significant at $P \leq 0.05$). On a percentage basis, live roots accounted for 51%, 43%, and 85%, respectively, of total root biomass beneath G, R, and M. The variability in live root biomass, and hence total root biomass, between plots was greatest beneath M, and least under R, as is apparent from the scatter around each plot mean (Fig. 4).

The biomass of dead roots beneath M (0.8 ± 0.2 kg/m²) tended not only to be lower but also much less variable compared to the either G (1.8 ± 1.1 kg/m²) or R (2.7 ± 1.2 kg/m²). The contrast between M and G, R was significant at $P \leq 0.05$; the contrast between R and M, G was significant at $P \leq 0.10$. Moreover, the distribution of dead root biomass in each of the two depth classes was much more uniform for M than for either of the other two cover types (CV% $> 100\%$ for 0–20 cm for both G and R). Indeed, the great variability in dead root biomass among plots under G and R makes inference about the abundance of dead root biomass rather difficult.

Table II lists, by plot, the biomass allocated to different root size classes. Thin root ($0.1 < \phi \leq 0.5$ cm) biomass was nearly identical beneath all three cover types, and it varied little within each type, irrespective of depth below ground. Aggregate (0–100 cm depth) thin root biomass was highest under G

(0.9 ± 0.1 kg/m²) and lowest under M (0.7 ± 0.1 kg/m²), but contrasts among cover types were not significant (all $P > 0.10$).

Medium roots ($0.5 \text{ cm} < \phi \leq 2.0 \text{ cm}$) had slightly less aggregate biomass than thin roots (mean 0.7 ± 0.4 kg/m² across all three cover types; Tab. II), but there was considerably more variability in medium root biomass within G and M, when compared to the distribution of thin root biomass. As with thin roots, there were no significant contrasts among cover types for medium roots (all $P > 0.10$).

The greater biomass in live roots under M (evident in Fig. 4b) clearly is due to the greater abundance of large and very large roots beneath this cover type (Tab. II). Mean large root ($2.0 \text{ cm} < \phi \leq 5.0 \text{ cm}$) biomass (averaged across all three cover types) was less than 0.5 kg/m², and was consistently low under R. Large root biomass under both G and M was somewhat larger but also more variable (0.5 ± 0.5 kg/m² under G and 0.8 ± 0.6 kg/m² under M), but there were no significant contrasts among cover types. Very large root ($\phi > 5.0$ cm) biomass was nonexistent under G and much lower under R (0.5 ± 0.5 kg/m²) than M (2.1 ± 1.6 kg/m²). The contrast M vs. G, R was significant at $P \leq 0.05$ for very large roots. The variability of very large root biomass under M was much greater than under either of the other two cover types.

Table II. Differences in root biomass (kg/m^2) among different cover types, according to root size class and depth. Cover types: G, Grassy opening; R, Regeneration clumps; M, Mature forest. Live root biomass is broken into different root diameter classes according to a system modified from Köstler et al. (1968): thin ($0.1 \text{ cm} < \phi \leq 0.5 \text{ cm}$), medium ($0.5 \text{ cm} < \phi \leq 2.0 \text{ cm}$), large ($2.0 \text{ cm} < \phi \leq 5.0 \text{ cm}$), very large ($\phi > 5.0 \text{ cm}$). A ‘–’ indicates that no roots of that size class were excavated from that particular pit.

Depth	Root class	Pit code								
		G1	G2	G3	R1	R2	R3	M1	M2	M3
0–20 cm	Dead	–	0.07	2.74	0.06	0.56	2.05	0.08	0.35	0.36
	Total live	2.37	1.04	0.71	1.95	1.13	1.59	3.55	0.89	2.94
	Thin	0.65	0.54	0.58	0.54	0.44	0.53	0.41	0.36	0.53
	Medium	0.82	0.14	0.13	0.40	0.36	0.34	0.91	0.42	0.28
	Large	0.90	0.35	–	0.16	0.34	–	0.24	0.11	1.52
	Very large	–	–	–	0.84	–	0.71	1.99	–	0.62
20–100 cm	Dead	1.45	0.96	0.28	1.29	3.00	1.18	0.52	0.58	0.40
	Total live	0.81	0.64	0.20	0.68	0.16	0.30	2.96	3.14	0.55
	Thin	0.25	0.40	0.18	0.38	0.12	0.21	0.35	0.26	0.27
	Medium	0.43	0.24	0.02	0.26	0.04	0.10	0.67	0.35	0.28
	Large	0.13	–	–	0.04	–	–	0.13	0.42	–
	Very large	–	–	–	–	–	–	1.81	2.10	–
Total (to 100 cm)	Dead	1.45	1.03	3.03	1.35	3.56	3.23	0.59	0.93	0.76
	Total live	3.18	1.68	0.91	2.63	1.29	1.89	6.51	4.03	3.49
	Thin	0.90	0.95	0.76	0.92	0.55	0.74	0.76	0.62	0.80
	Medium	1.25	0.38	0.15	0.67	0.39	0.44	1.58	0.78	0.55
	Large	1.02	0.35	–	0.20	0.34	–	0.37	0.53	1.52
	Very large	–	–	–	0.84	–	0.71	3.80	2.10	0.62
Total live + dead	4.63	2.71	3.93	3.99	4.85	5.12	7.11	4.96	4.25	

3.2. Root biomass by depth horizon

Summed across all four root size classes, and averaged across all three cover types, 63% of total (to a depth of 100 cm) live root biomass was contained in the 0–20 cm soil horizon, suggesting a fairly shallow rooting habit (Tab. II). However, this mean value hides the tremendous variability both within and among cover types. For example, for both G (mean 72%) and R (mean 80%), between 62% and 88% of the total live root biomass of each plot was contained in the upper soil horizon, whereas for M (mean 53%), the range was from 22% to 84%. Within the different root size classes, greater disparities were apparent. For example, whereas there was consistently 60–70% of total thin root biomass in the 0–20 cm horizon, the distribution of very large roots was much more highly variable. For one plot under M (and two plots under R), all very large root biomass was in the 0–20 cm horizon, whereas for another plot under M, all very large root biomass was in the 20–100 cm horizon. In contrast, none of the plots under G had any very large root biomass, in either of the horizons sampled (Tab. II).

4. DISCUSSION

Live root biomass may vary by as much as two orders of magnitude across the world’s biomes, from 0.2 to 20 kg/m^2 [2, 8]. Jackson et al. (1996) [8] estimated an average root biomass in temperate coniferous forests of 4.4 kg/m^2 . In our stands, due mainly to differences in large and very large root biomass among cover types, total live root biomass averaged 4.7 kg/m^2 under M, but was only 1.9 kg/m^2 under both G and R (the greater biomass under M compared to R is consistent with the idea that larger and more dominant trees contribute disproportionately to total below ground biomass in a stand [11]). Total

root biomass in a mixed-conifer (mostly Douglas-fir) forest in New Mexico was reported to be $4.4 \pm 0.7 \text{ kg/m}^2$, with $\phi \leq 0.5 \text{ cm}$ root biomass accounting for $0.4 \pm 0.1 \text{ kg/m}^2$ [5]. Root ($\phi < 0.5 \text{ cm}$) biomass of Douglas-fir in Oregon ranged from 0.8 – 1.0 kg/m^2 [18], comparable to the average (across all three cover types) of 0.8 kg/m^2 for thin root biomass at Pothole Creek. In spite of the fact that root biomass is known to vary considerably depending on species, climate, and soil conditions [2, 8], our estimates are more or less in keeping with these other studies.

In both G and M, roots with $\phi > 0.5 \text{ cm}$ accounted for the majority of total live root biomass, as has been shown for *Fagus sylvatica* [11]. For example, thin roots in M accounted for just 16% of total live root biomass.

Whereas temperate grasslands generally have 69% of root biomass in the top 20 cm of soil, temperate coniferous forests typically have only 38% in the top 20 cm [8]. Along with deserts, temperate coniferous forests have the deepest rooting profiles. At the Pothole Creek site, the top 20 cm of soil had a much higher percentage of total live root biomass, ranging from 53% under M to 80% under R. Root density under M at the Pothole Creek site (12.3 kg/m^3 in the 0–20 cm horizon) was about twice as high as that reported by Jackson et al. (1996) [8] for temperate coniferous forests; root density under G (6.9 kg/m^3 in the 0–20 cm horizon) was similar to that reported for temperate grasslands in the same study. Overall, the rooting profiles at Pothole Creek are quite shallow, especially in light of the fact that within the IDF zone, growing season moisture deficits are quite common [13].

Past results in both tropical [16, 17], and temperate [1, 22] forests have shown that tree fall gaps not only result in canopy openings, but also in the development of below-ground ‘root

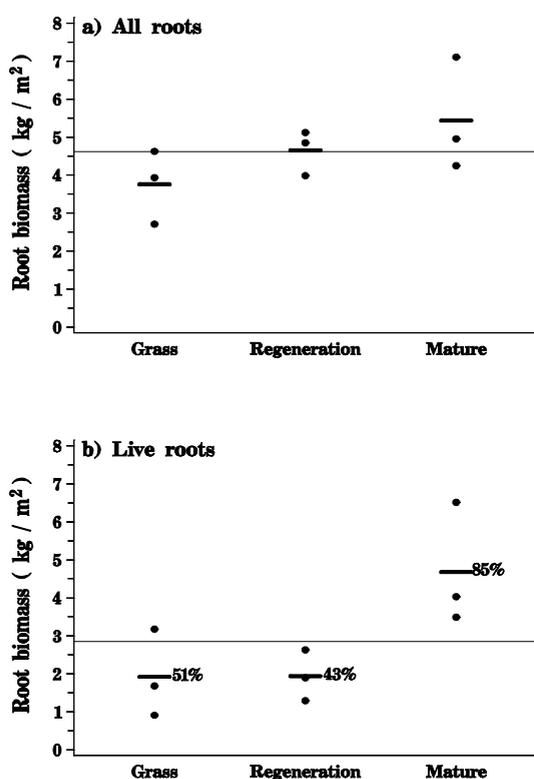


Figure 4: (a) Total (live + dead) and (b) live root biomass (kg/m^2) in each of the nine pits excavated, separated by cover type. Faint horizontal lines indicate the mean value across all three cover types. Heavier, short lines indicate means within each cover type. In Figure 4b, values next to each mean indicate the percentage of total root biomass that was accounted for by live roots within that cover type.

gaps”, which are characterized by a sharp (but transitory) reduction in fine root abundance. It is likely that the selective harvest some 30 years ago at Pothole Creek also resulted in some sort of “root gap” beneath the canopy openings. However, the similarity of thin root biomass across all three cover types in the present study suggest that although the canopy openings over G remain to this day, there are no corresponding root gaps. We believe that our data support the idea that significant root competition is occurring at Pothole Creek: root competition from pinegrass appears to be sufficiently intense that tree regeneration is suppressed or out-competed.

The connection between canopy openings and root gaps is of great importance to silviculturists utilizing either partial cutting or selection systems, where a primary concern is that regeneration must be established before the available growing space can be occupied by competing vegetation [20]. Directly related to the present study, Petersen (1988) [14] demonstrated the effects of pinegrass on *Pinus ponderosa* growth at a dry, interior site in Montana, USA. Based on the results presented here, we suggest that future management of sites similar to Pothole Creek may necessitate (1) harvesting methods that discourage grass invasion without discouraging natural tree regeneration; or (2) prompt execution of artificial regeneration (such as underplanting) to avoid excessive competition from grass or shrubs.

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