ROOTING PATTERNS

OF BOREAL MIXEDWOOD SPECIES

IN SASKATCHEWAN

A Report for the

Prince Albert Model Forest

Ken Van Rees/Doug Jackson

Soil Science Department

University of Saskatchewan

March 1994

TABLE OF CONTENTS

Chapter **Page**

TABLE OF CONTENTS i

LIST OF TABLES ii

LIST OF FIGURES iii

Introduction 1

Material and Methods 2

Results 7

Discussion 23

Conclusions 30

References 31

LIST OF TABLES

Table **Page**

Table 1. Number of trees within a three m radius of soil core. 8
Table 2. Soil description for each increment in the core. 9
Table 3. Soil texture for each increment in the core. 10
Table 4. Soil physical and chemical data for the three soil types. 11
Table 5. Total root length (cm) per soil core. 12
Table 6. Percentage (%) of root length in each core for each species. 14
Table 7. Percentage (%) of root length in different soil horizons 20
Table 8. Percentage of root length in various diameter classes. 21
Table 9. Total root weight (g) per soil core. 22

LIST OF FIGURES

Figure **Page**

Figure 1. Map of the Prince Albert Model Forest and the location of the research site (x)......................... 3
Figure 2. Distribution of soils at the research site... 4
Figure 3. Elevational map of research site and location of sampled cores. 5
Figure 4. View of vegetation in the Mixedwood stand at the research site. 6
Figure 5. Root length density of all species combined for each major soil type. 13
Figure 6. Root length density by species for the Mixedwood stand on the Brunisol soil......................... 16
Figure 7. Root Length density by species for the Mixedwood stand on the Luvisol soil......................... 17
Figure 8. Root Length density by species for the Mixedwood stand on the Gleysol soil......................... 18
Figure 9. Root length density by species for the jack pine stand growing on the Brunisol soil. 19
Figure 10. Root weight density for all species combined for the major soil types.................................. 24
Figure 11. Root weight density by species for the Mixedwood stand on the Brunisol soil...................... 25
Figure 12. Root weight density by species for the Mixedwood stand on the Luvisol soil. 26
Figure 13. Root weight density by species for the Mixedwood stand on the Gleysol soil. 27
Figure 14. Root weight density by species for the jack pine growing on the Brunisol soil...................... 28

Introduction

Concern has been raised as to the impacts of harvesting and site preparation methods and in some cases fire events on the nutrient status of forest soils. Some forestry practices can be detrimental to nutrient levels in the soil by either removing surface mineral soil and litter layers such as in landings or through increased nutrient leaching following harvesting; hence reducing the productivity of a site for future tree rotations. The role of tree roots in capturing nutrients that may be potentially lost to nutrient leaching is not understood and Gale and Grigal (1987) suggested that early successional species (i.e., aspen) may be beneficial in minimizing nutrient loss due to their extensive root systems whereas late successional species (i.e., spruce) are better suited for sites where nutrient resources are concentrated near the soil surface. In the Boreal Mixedwood forests, however, little is known about the distribution and extent of aspen and spruce roots and where roots of each species exploit the soil profile for water and nutrients.

Root length measurements are necessary in order to understand the role of roots in the absorption of water and nutrients, especially from the standpoint of investigating nutrient competition between species. Roots that are actively involved in uptake are generally less than 3 mm in diameter. There are no studies, however, that have quantified root length densities for aspen and spruce in Boreal Mixedwood stands. Strong and La Roi (1983a) did quantify the number of roots on soil pit faces for various boreal species, but did not separate out species or determine root length densities. There has been some work done in Minnesota on root distributions of aspen in pure aspen stands (Ruark and Bockheim, 1987), but not a mixedwood stand.

The objective of this project (1993-1994) is to investigate the rooting distribution of mature aspen and spruce trees in a Boreal Mixedwood forest located in Prince Albert National Park. Future work will determine the activity of these root systems in different parts of the soil profile using a stable tracer.

Material and Methods

The site was located in the Prince Albert National Park (UTM coordinates: 13U 425840 5968800 SW corner) which is a part of the Prince Albert Model Forest (PAMF) (Fig. 1). This area is associated with the Waskesiu Hills Upland (rolling topography) and is a part of the Populus-Aralia/Linnaea ecosystem in the Mixedwood ecodistrict (Kabzems *et al*., 1986).

The general landscape is classified as a Loon River-Bittern Lake with a slope class of 35 %. The research plot is dominated by Loon River (orthic Gray Luvisolic) soils over 70 % of the landscape with significant inclusions of Bittern Lake (Brunisolic Gray Luvisols, Eutric Brunisolic soils, and gleyed variants of the Luvisolic and Brunisolic orders in lower landscape positions) (Fig. 2). An elevational map for the area (produced by Dr. D. Pennock) and the location of the sampling sites is presented in Figure 3.

The vegetation on the site consists predominantly of mature trembling aspen (*Populus tremuloides* Michx.; tA) and white spruce (*Picea glauca* (Moench) Voss; wS) with some balsam poplar (*Populus balsamifera* L.; bPo) growing on the Gleysols. Understory vegetation consisted of prickly rose (*Rosa acicularis*), dry-spike sedge (*Carex siccata* Dewey), and bearberry (*Arctostaphylos uva-ursi* (L.) Spreng) (Fig. 4). Stocking of the stand was ≈ 2000 stems ha^{-1}. Another site down the haul road with jack pine (*Pinus banksiana* Lamb; jP) was also selected to take two cores for jack pine root length.

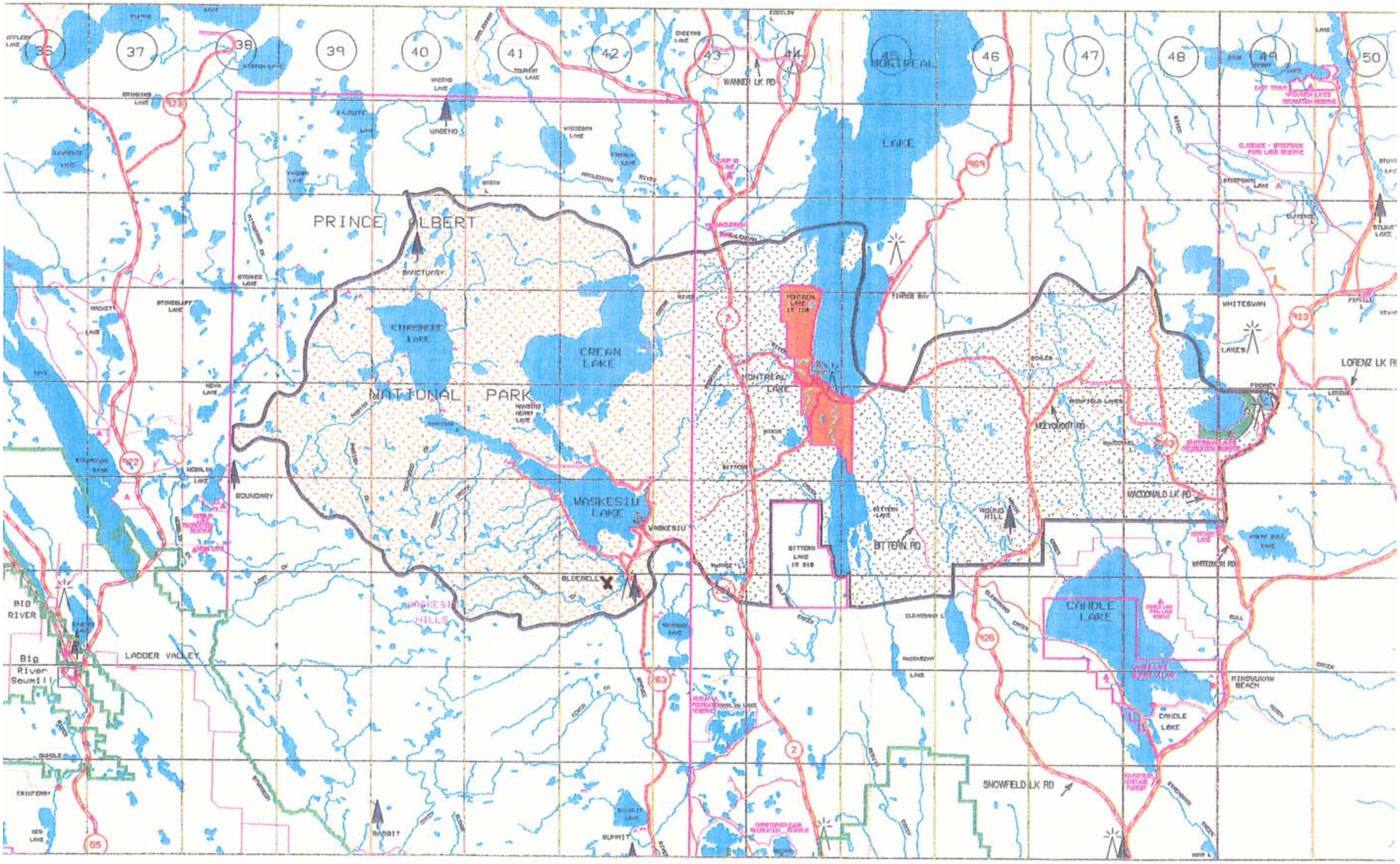

Figure 1.
Map of the Prince Albert Model Forest and the location of the research site (x).

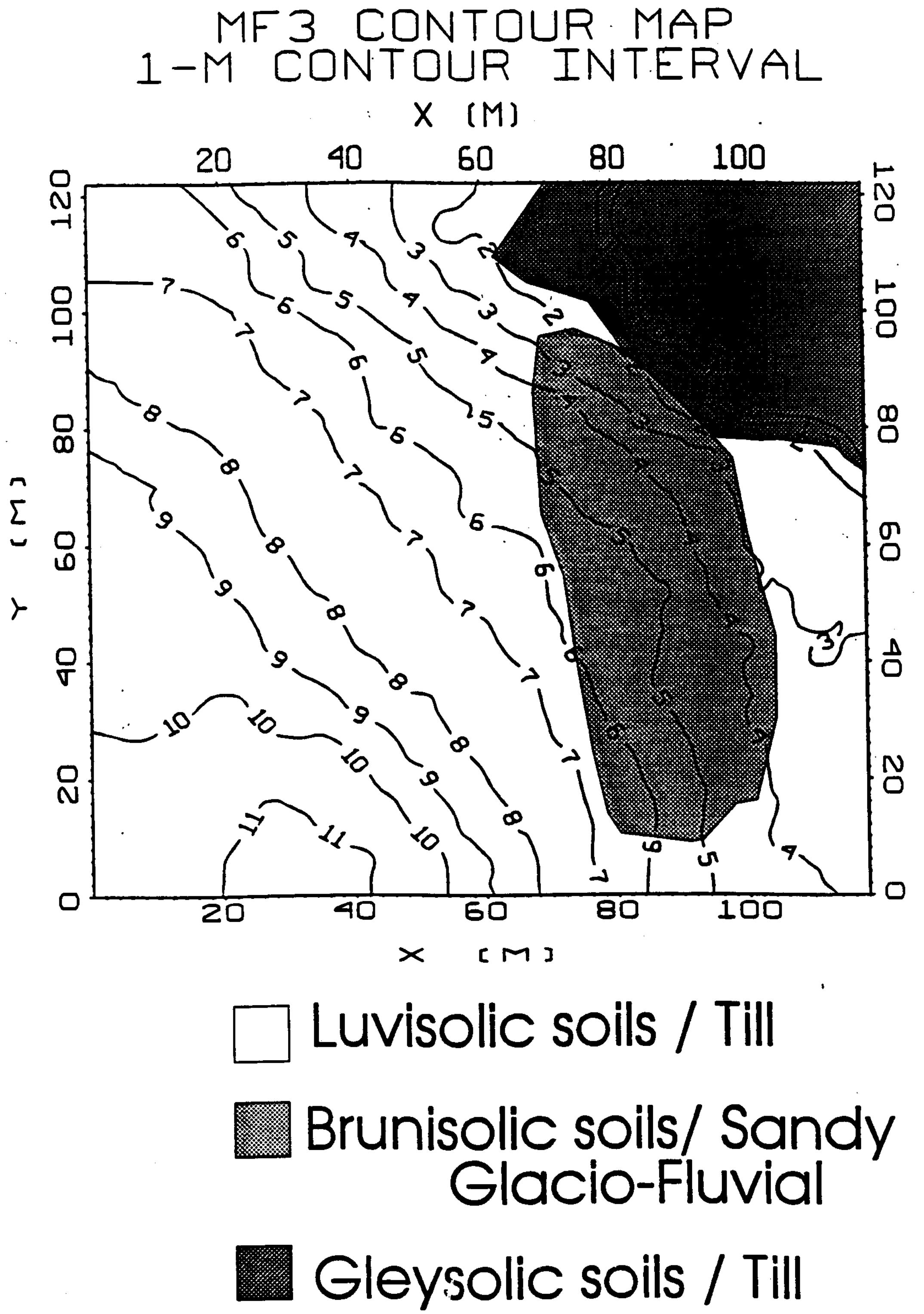

Figure 2.
Distribution of soils at the research site.

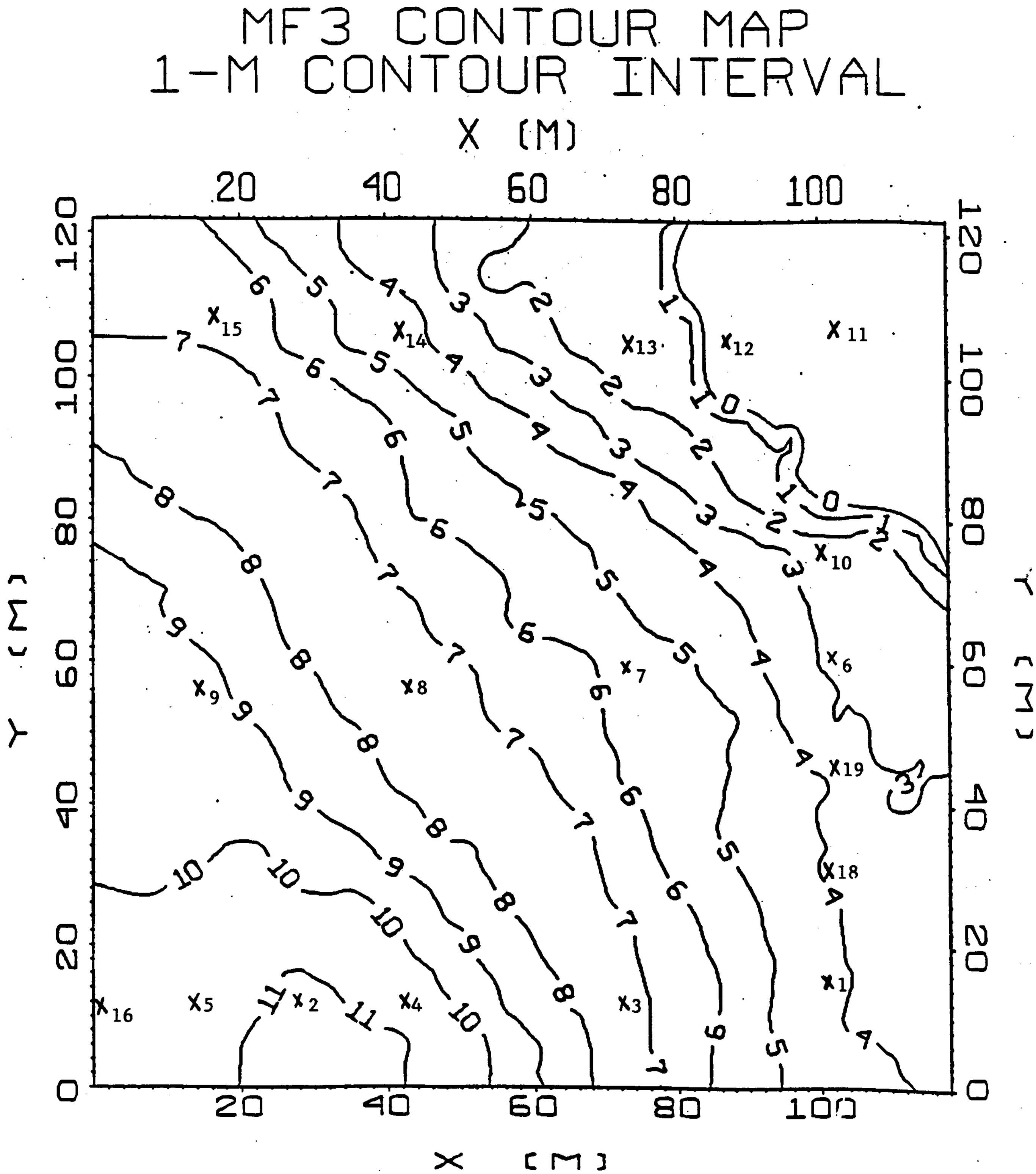

Figure 3.
Elevational map of research site and location of sampled cores.

Figure 4.
View of vegetation in the Mixedwood stand at the research site.

Soil cores for root distributions were taken from selected landscape positions to cover a range in soil type and landscape elements. The first 0 to 15 cm increment was taken with a root auger, and the remaining 15 cm increments to 120 cm depth by a Riverside auger. Samples were stored at 4°C until processing. Soil samples were placed in meshed bags and rinsed in water to remove the soil; roots were then frozen until root lengths could be counted. Soil samples with high amounts of clay were soaked in water and frozen in order to disperse the clay aggregates prior to washing. Roots were separated by species (aspen, white spruce, grass and other [understory species]) and diameter class (< 2, 2-5 and > 5 mm). Root lengths were counted using the line-intercept technique (Newman, 1966) and the samples were then ovendried. The number and type of tree was also recorded within a 3 m radius of each core (Table 1). Profile descriptions and soil texture for each depth and core are presented in Tables 2 and 3, respectively. Median soil nutrient data for the major soil types in the mixedwood stand were determined by Dr. Pennock's group and are presented in Table 4.

Results

Mean total root length per core was highest for the Brunisol soil and lowest for the Luvisol when looking at the aspen/spruce site; however, the mean total root length per core for the jack pine growing on the Brunisol soil was half of the root length found for the Luvisol (Table 5). Per unit root length density, Brunisols had higher densities in the forest floor but densities in Gleysols tended to be somewhat higher in the subsoils (Fig. 5). Despite textural differences between the three soils, root length densities were very similar in the mineral soil. There appeared to be no relationship between the soil chemical data for each soil and the root distributions.

Table 1.
Number of trees within a three m radius of soil core.

Soil Type	Core	tA	bPo	wS	Understory ‡
Luvisol	2	4	0	1	gr
	3	2	0	2	moss
	4	3	0	0	gr, stb,
	5	2	0	3	mos, ltea, blueb
	6	7	0	0	rose, gr, blueb
	7	7	0	4	bearb, moss
	8	5	0	1	moss, gr, bearb
	9	6	0	0	gr, moss, stb
	15	4	0	4	ltea, moss, blueb
	16	0	0	3	moss, bunb, bearb
	19	6	0	0	gr
Brunisol	1	6	0	0	blueb, gr, bearb
	10	0	0	2	rose, gr, stb
	13	3	1	2	gr, rose
	14	5	0	0	gr, stb, bearb
	18	5	0	0	gr, bearb, blueb
Gleysol	11	6	4	0	moss, stb, rose
	12	1	3	13 (small)	rose, moss
Brun jP	20	0	0	5†	moss, bearb
	21	0	0	7	moss, bearb

† White spruce is jack pine for this soil
‡ gr-sedge, stb-strawberry, bearb-bearberry, ltea-labrador tea, blueb-blueberry

Table 2.
Soil description for each increment in the core.

Core	Thickness LFH (cm)	0-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120
	---------- Luvisols ----------								
2	4	Ae	Ae	Ae/Bt	Bt	Bt	C	C	C
3	2	Ae	Ae	Bt	Bt	C	C	C	
4	2.5	Ae	Ae	Bt	Bt	Bt	C	C	C
5	4	Ae	Ae	Bt	Bt	Bt	Ck	Ck	Ck
6	3	Ae	Bt	CkI	Ckl	CII	CII	CII	CII
7	4	Ae	Ae	Ae/Bt	Bt	Ck	Ck	Ck	Ck
8	3	Ae	Bt	Bt	Bt	Bt			
9	4	Ae	Ae	Bt	Bt	Bt	Ck	Ck	Ck
15	4	Ae	Ae	Bt/Ae	Bt	Ck/Bt	Ck	Ck	Ck
16	3	Ae/Ah	Bt	Bt	Bt				
19	4	Ae	Bt/Ae	Bt	Bt	Bt	Ck	Ck	Ck
	---------- Brunisol ----------								
1	3.5	Bm	Bm	C	C	C			
10	7	Bm	Bm	Bm	C	C	C	C	C
13	6	Bm	Bm	Ck/Bm	Ck	Ck	CII	CII	CII
14	7	Ae	Bm	Bm	Bm	C	C	C	
18	4	Bm	Bm	Bm	BC	BC			
	---------- Gleysol ----------								
11	13	Ah	Ae	CgI	CgI	CgI	CgI/CgII	CgII	CgII
12	5	Ah	Ahk	Cg	Cg	Cg	Cg	Cg	Cg
	---------- Brunisol-jP ----------								
20	4	BmI	BmI	Bml	BmII	BmII	BmII	C	C
21	1	BmI	BmI	BmII	BmII	BmII	C	C	C

Table 3.
Soil texture for each increment in the core.

Core	0-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120
				Luvisols				
2	sl	sl	sl/s-scl	scl	scl	scl	scl	scl
3	sl	sl	scl	scl	scl	scl	scl	
4	sl	sl	scl-cl	scl-cl	scl	scl	scl	scl
5	fl	fl	cl	cl	cl	scl	scl	scl
6	sl	scl	sil	sil	s	s	s	s
7	sl	sl	sl/s-cl	cl	cl	cl	cl	cl
8	1	cl	cl	cl	cl			
9	1	1	scl-cl	scl-cl	scl-cl	scl-cl	scl-cl	scl-cl
15	sl	sl	scl/sl	scl	scl-cl	scl-cl	scl-cl	scl-cl
16	1	scl	scl	scl				
19	ls	scl/ls	scl	scl	scl	scl-cl	scl-cl	scl-cl
				Brunisol				
1	s	s	s	s	s			
10	s	s	s	s	s	s	s	s
13	s	s	sicl/ls	sicl	sicl	s/s-cl	s/s-cl	s/s-cl
14	ls	ls	ls	sl/s-1	sl	ls	ls	
18	s	s	s	s	s			
				Gleysol				
11	s	s	sicl/1-s	sicl	sicl	s/s-cl	s/s-cl	s/s-cl
12	1	scl-cl	scl-cl	scl-cl	scl-cl	scl-cl	scl-cl	scl-cl
				Brunisol-jP				
20	s	s	sl	sl/s-cl	sl/scl	sl/s-cl	s	s
21	s	s	sl/s-cl	sl/s-cl	sl/s-cl	s/1-scl	s	s

Table 4.
Soil physical and chemical data for the three soil types.

Soil	**Depth (cm)**	**Bulk Den g cm^{-3}**	**pH**	**Total N (%)**	**NH_4 $\mu g\ g^{-1}$**	**NH_3 $\mu g\ g^{-1}$**
Luvisol	0-15	1.15	5.6	0.11	5.25	0.14
	15-30	1.69	6.0	0.03	4.56	0.13
	30-45	1.77	6.2	0.03	3.41	0.04
Brunisol	0-15	1.17	5.6	0.14	6.85	0.15
	15-30	1.81	6.4	0.04	6.84	0.16
	30-45	1.79	6.6	0.04	6.54	0.03
Gleysol	0-15	0.90	5.4	0.25	5.00	0.14
	15-30	1.51	6.8	0.08	5.95	0.09
	30-45	1.52	7.2	0.04	6.22	0.04

Table 5.
Total root length (cm) per soil core.

Soil Type	Core	Depth (cm)	tA	wS	Grass	Other	Total
Luvisol	2	120	1851.2	0	212.7	829.8	2893.7
	3	105	2335.2	431.1	0	159.9	2923.2
	4	120	1835.4	249.5	447.9	483.9	3016.8
	5	120	2106.7	264.6	0	494.8	2866.1
	6	120	2075.6	0	853.2	424.5	3353.3
	7	120	3371.8	151.5	188.4	100.5	3812.2
	8	75	2664.3	36.0	0	661.5	3361.8
	9	120	1571.6	0	334.9	80.4	1986.9
	15	120	694.1	432.9	227.7	327.4	1682.1
	16	60	113.9	488.9	0	309.8	912.7
	19	120	1479.5	0	1056.4	24.3	2560.2
Brunisol	1	75	2444.9	0	940.3	1365.6	4750.9
	10	120	1962.6	283.0	845.7	401.9	3493.2
	13	120	1953.4	335.8	263.8	343.3	2896.2
	14	105	3561.1	13.4	380.1	419.5	4360.7
	18	75	2141.8	0	320.7	175.8	2638.3
Gleysol	11	120	1666.2	0	1595.1	488.1	3749.4
	12	120	1935.8	228.6	0	1179.8	3344.2
Brun-jP	20	120	0	1122.8†	0	1058.3	2181.2
	21	120	0	334.1	0	181.7	515.8

† White spruce is jack pine for this soil

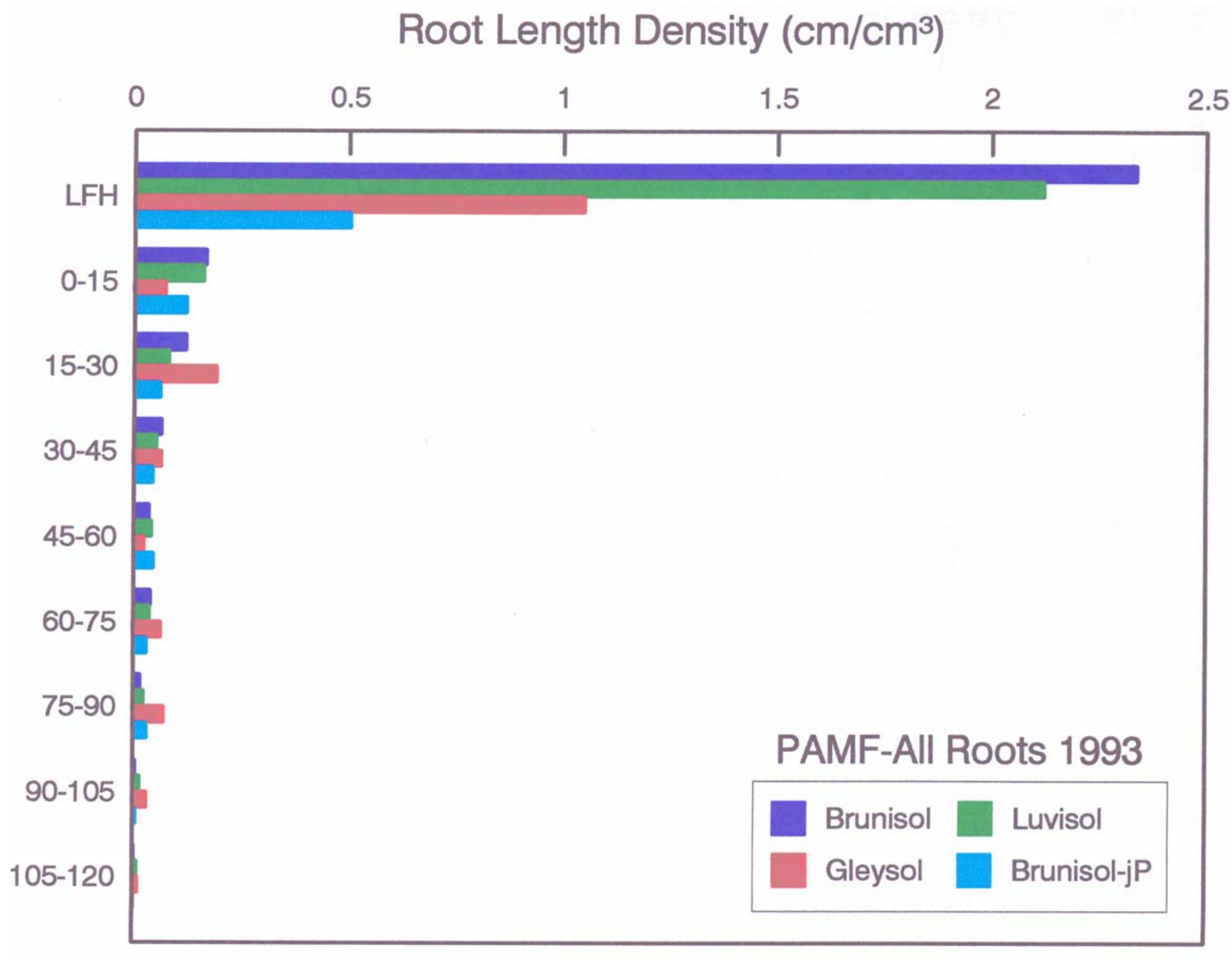

Figure 5.
Root length density of all species combined for each major soil type.

Table 6.
Percentage (%) of root length in each core for each species.

Soil Type	White Spruce	Trembling Aspen	Grass	Other
Luvisol	6.9	69.8	9.8	13.5
Brunisol	3.4	64.2	16.1	16.3
Gleysol	5.7	52.1	18.8	23.4
Brun-jP	39.9†	-	-	60.1

† White spruce is jack pine for this soil

Trembling aspen was the dominant species accounting for 52 to 70% of the root length for the three major soils (Table 6). White spruce only accounted for 4 to 7% of the total root length and grasses and other roots had root length densities that were 1.4 to 4.7 and 2.0 to 4.8 times higher, respectively than the white spruce root length. Grass and other root lengths were higher on the wetter Gleysol soil than for the Luvisol and Brunisol soils.

Root length densities by soil depth for the mixedwood stand on the Brunisol, Luvisol, Gleysol and jack pine on the Brunisol are presented in Figures 6, 7, 8 and 9, respectively. Root length densities were highest in the LFH layer and generally decreased with soil depth (Figs. 6-9). Roots were found to a 120 cm soil depth. The LFH layer accounted for 51 to 94% of the white spruce root length and 55 to 63 % of the trembling aspen root length (Table 7). Jack pine root length densities in the LFH, however, accounted for only 14 % of the total root length (Table 7). Although the Gleysols represent only two cores, there was a significant increase in other root length at the 15 to 30 cm depth and also an increase in trembling aspen root length density at depths greater than 60 cm. Root length at depths greater than 60 cm contributed up to 15 and 26% of white spruce and trembling aspen root length, respectively (Table 7).

Fine root length (< 2 mm dia.) comprised from 94 to 100% of the total root length for all species in the four soil types (Table 8). The larger diameter roots were associated with spruce, aspen and jack pine.

There was a slight correlation between total length of spruce roots in the LFH and the number of trees within a 3 m radius of the soil core (Rtl = 21.4 + 57.8(# trees), $r^2 = 0.59$); however, no significant correlation could be found for trembling aspen (Rtl = 465.7 + 140.4(# trees), $r^2 = 0.21$).

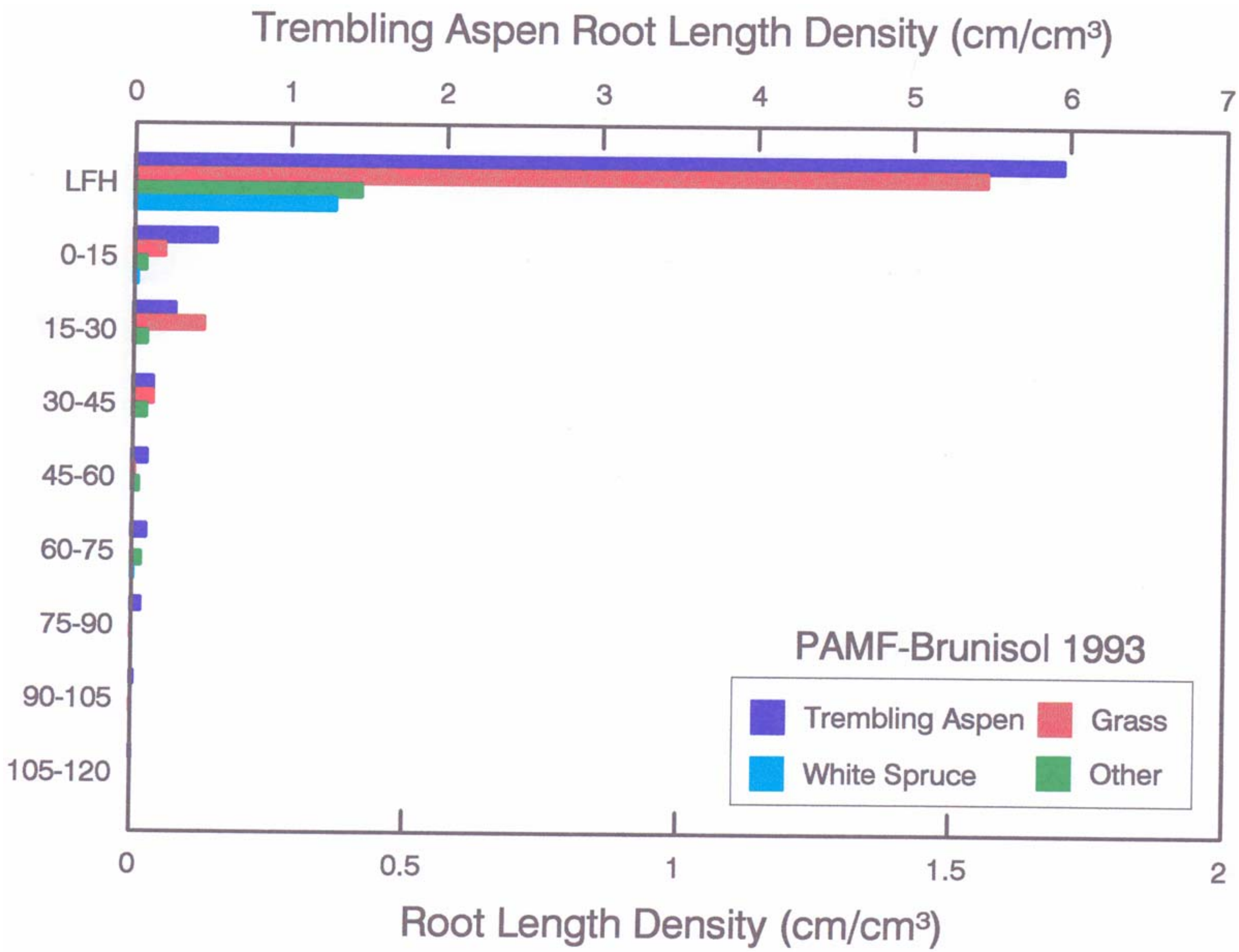

Figure 6.
Root length density by species for the Mixedwood stand on the Brunisol soil

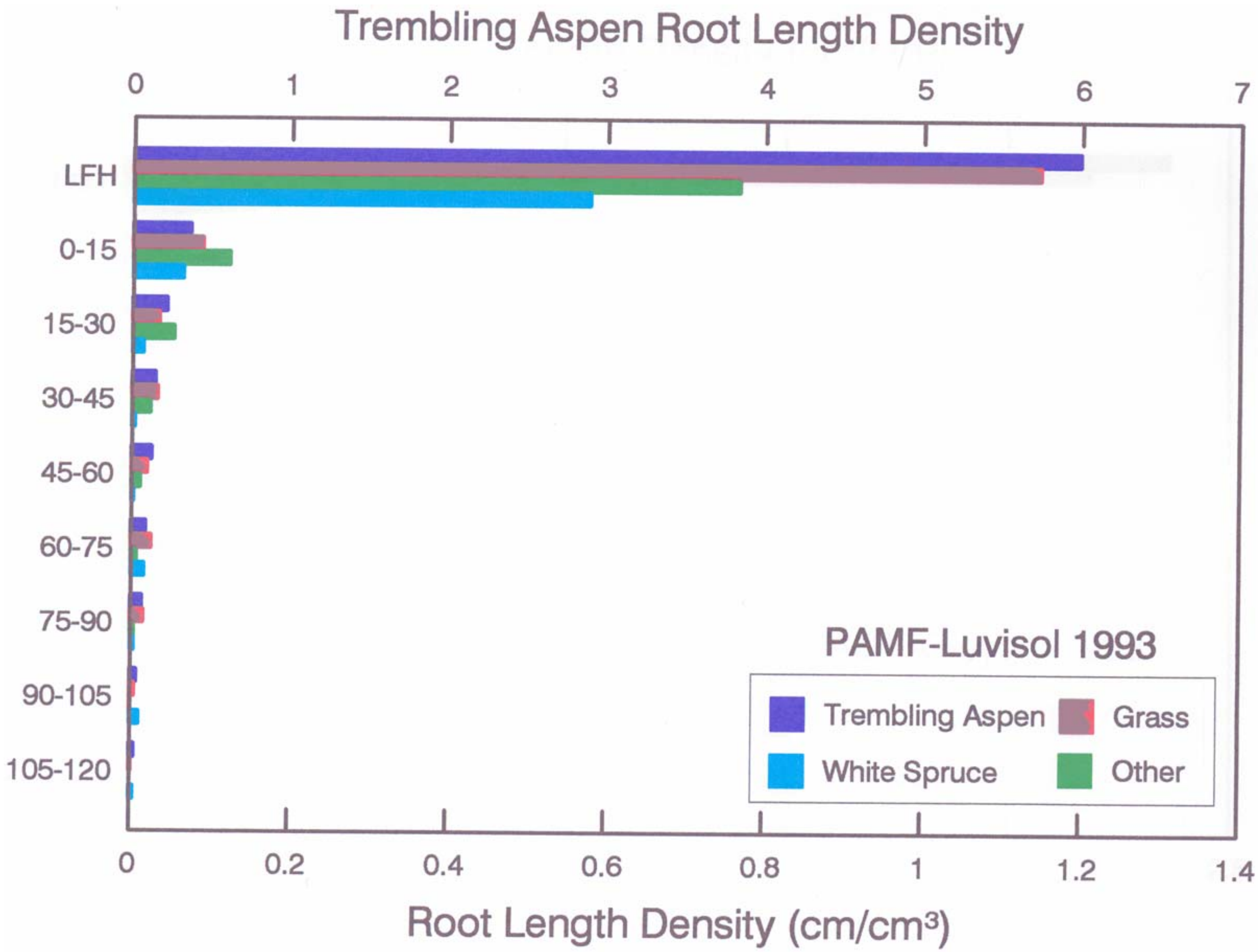

Figure 7.
Root Length density by species for the Mixedwood stand on the Luvisol soil.

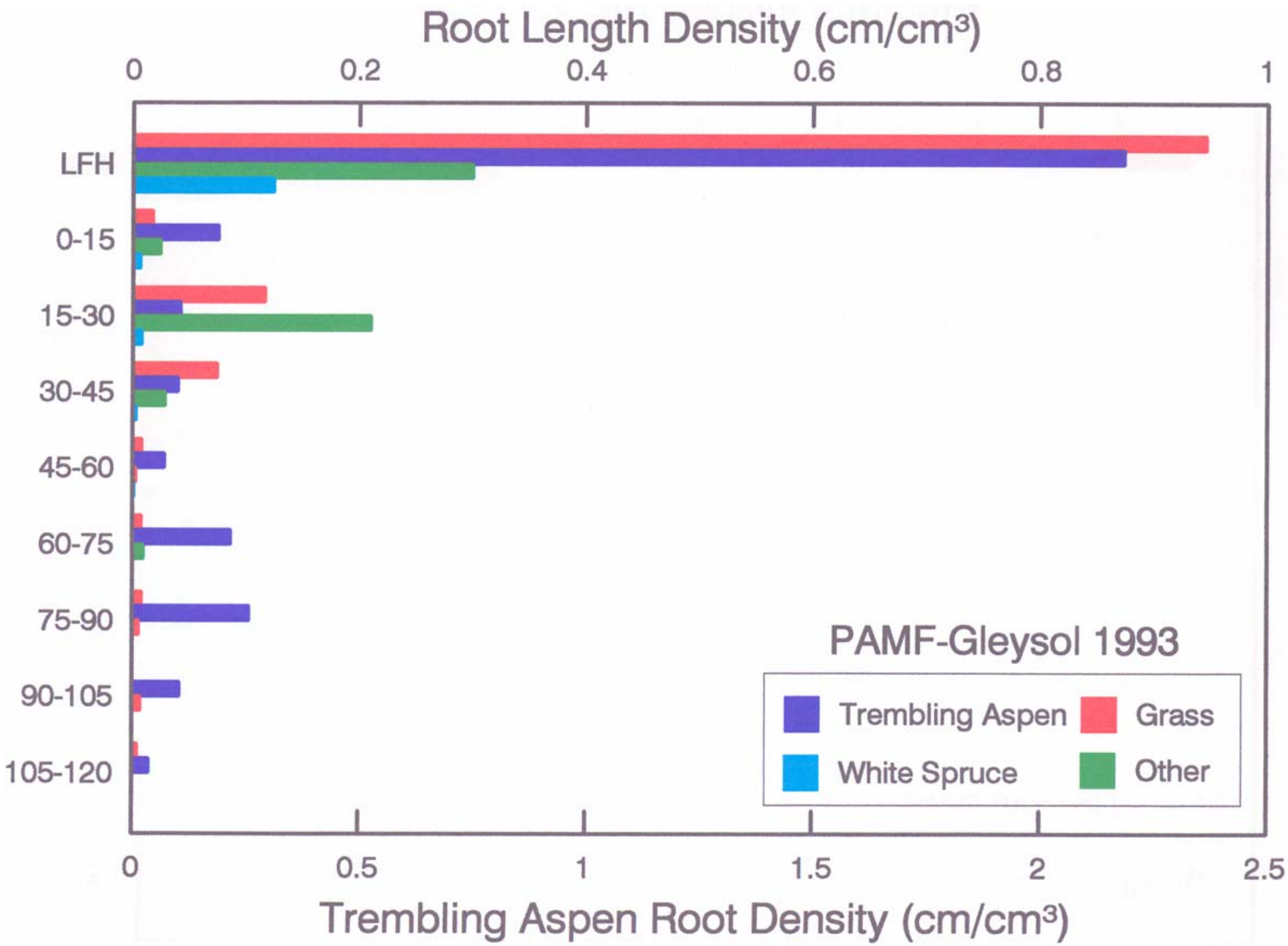

Figure 8.
Root Length density by species for the Mixedwood stand on the Gleysol soil.

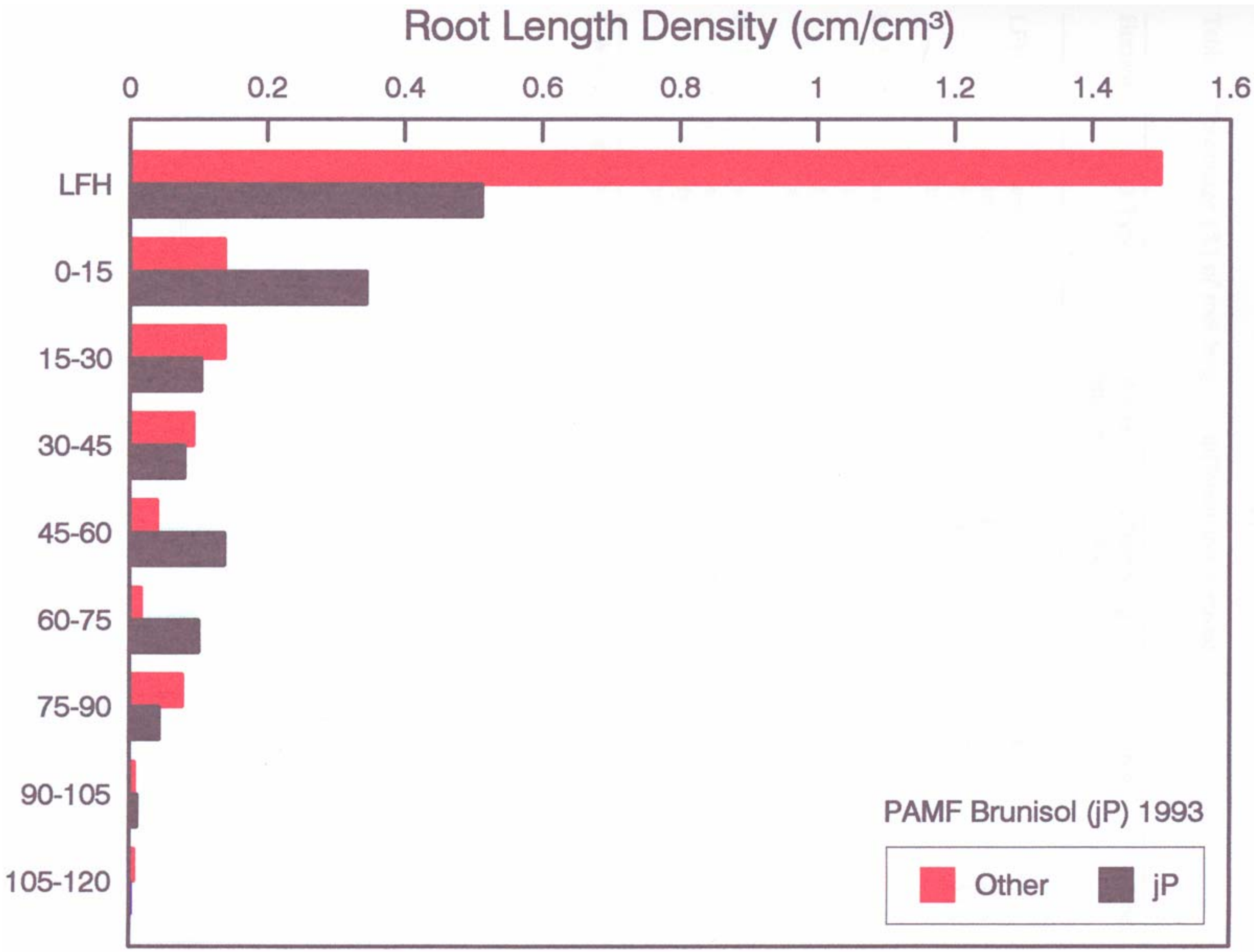

Figure 9.
Root length density by species for the jack pine stand growing on the Brunisol soil.

Table 7.
Percentage (%) of root length in different soil horizons

Horizon	Soil Type	White Spruce	Trembling Aspen	Grass	Other
LFH	Luvisol	51	55	44	52
	Brunisol	94	63	69	56
	Gleysol	69	55	77	35
	Brun-jP	14†	-	-	36
0-15 cm	Luvisol	26	15	31	19
	Brunisol	4	16	8	9
	Gleysol	11	8	2	6
	Brun-jP	36†	-	-	17
60-120 cm	Luvisol	15	9	3	10
	Brunisol	2	5	0	8
	Gleysol	0	26	2	5
	Brun-jP	16†	-	-	14

† White spruce is jack Pine for this soil

Table 8.
Percentage of root length in various diameter classes.

Soil Type	Species	< 2 mm	2-5 mm	> 5 mm
Luvisol	Spruce	93.9	6.1	0
	Aspen	97.3	0.8	1.9
	Grass	100	0	0
	Other	99.8	0.2	0
Brunisol	Spruce	98.0	2.0	0
	Aspen	98.8	0.6	0.6
	Grass	100	0	0
	Other	98.9	0	1.1
Gleysol	Spruce	100	0	0
	Apen	98.1	1.1	0.7
	Grass	100	0	0
	Other	100	0	0
Brunisol-jP	Pine	93.9	3.7	2.4
	Other	100	0	0

Table 9.
Total root weight (g) per soil core.

Soil Type	Core	Depth (cm)	tA	wS	Grass	Other	Total
Luvisol	2	120	3.909	0.000	0.177	0.336	4.422
	3	105	5.200	1.959	0.000	0.159	7.318
	4	120	13.195	0.307	0.146	0.353	14.001
	5	120	5.192	4.564	0.000	0.236	9.992
	6	120	11.298	0.000	0.340	0.370	12.008
	7	120	4.759	0.105	0.099	0.093	5.056
	8	75	4.072	0.012	0.000	0.353	4.437
	9	120	27.869	0.000	0.141	0.262	28.272
	15	120	2.472	1.040	0.135	0.248	3.895
	16	60	0.166	1.901	0.000	0.318	2.385
	19	120	15.359	0.000	0.548	0.293	16.200
Brunisol	1	75	2.911	0.000	0.357	14.596	17.864
	10	120	2.678	0.833	0.161	0.393	4.065
	13	120	5.434	0.734	0.323	0.404	6.895
	14	105	6.094	0.007	0.211	0.202	6.514
	18	75	6.478	0.000	0.089	3.356	9.923
Gleysol	11	120	1.456	0.000	0.433	0.599	2.488
	12	120	9.309	0.297	0.000	1.441	11.047
BrunjP	20	120	0.000	3.835†	0.000	0.670	4.505
	21	120	0.000	5.096	0.000	0.201	5.297

† White spruce is jack Pine for this soil

The majority of the root weight for each core was in the aspen roots (Table 9). The weight of pine roots per core was 5 and 14 times higher than that for spruce roots in the Luvisol and Brunisol soils, respectively. Gleysols had the highest root weight densities in the LFH layer, but declined significantly in the mineral soil compared to the other soil types (Fig. 10). Root weight densities were higher in the mineral horizons on the Luvisol soils. With respect to species, root weight densities were highest for aspen in the LFH layer for the Brunisol (Fig. 11) and Luvisol (Fig. 12) soils; however, other root weight density was larger than aspen on the Gleysol (Fig. 13) soil and higher than jack pine growing on the Brunisol (Fig. 14).

Discussion

This study represents the first attempt to quantify root length and weight densities for a boreal mixedwood stand in Canada. Fine roots were found to a 1.2 m depth for all soil types and this compares with rooting depths in the literature for aspen stands which ranged from 1.5 to > 3 m and from 1.4 to 3 m for white spruce stands (Stone and Kalisz, 1991). Schultz (1969) also reported that taproots or sinkers of natural white spruce stands in Michigan, Wisconsin and Minnesota penetrated, on average to 0.92 m, with one sinker found to 1.8 m. White spruce roots penetrated deeper on sands than on sandy-loams and silt-loam soils (Schultz, 1969). Jack pine taproots have been found to a depth ranging from 1.0 to 2.9 m (Bannan, 1940; Strong and La Roi, 1983b; Stone and Kalisz, 1991).

Fine root biomass expressed on an hectare basis for aspen in this study ranged from 2.89 to 55.46 Mg ha^{-1} with an average of 14.13 Mg ha^{-1} across all soils. This average is comparable to the estimate of 10.7 Mg ha^{-1} found for roots (< 30 mm dia.) of a 63 year old aspen stand by Ruark and Bockheim (1988). Belowground biomass for understory species (excluding spruce)

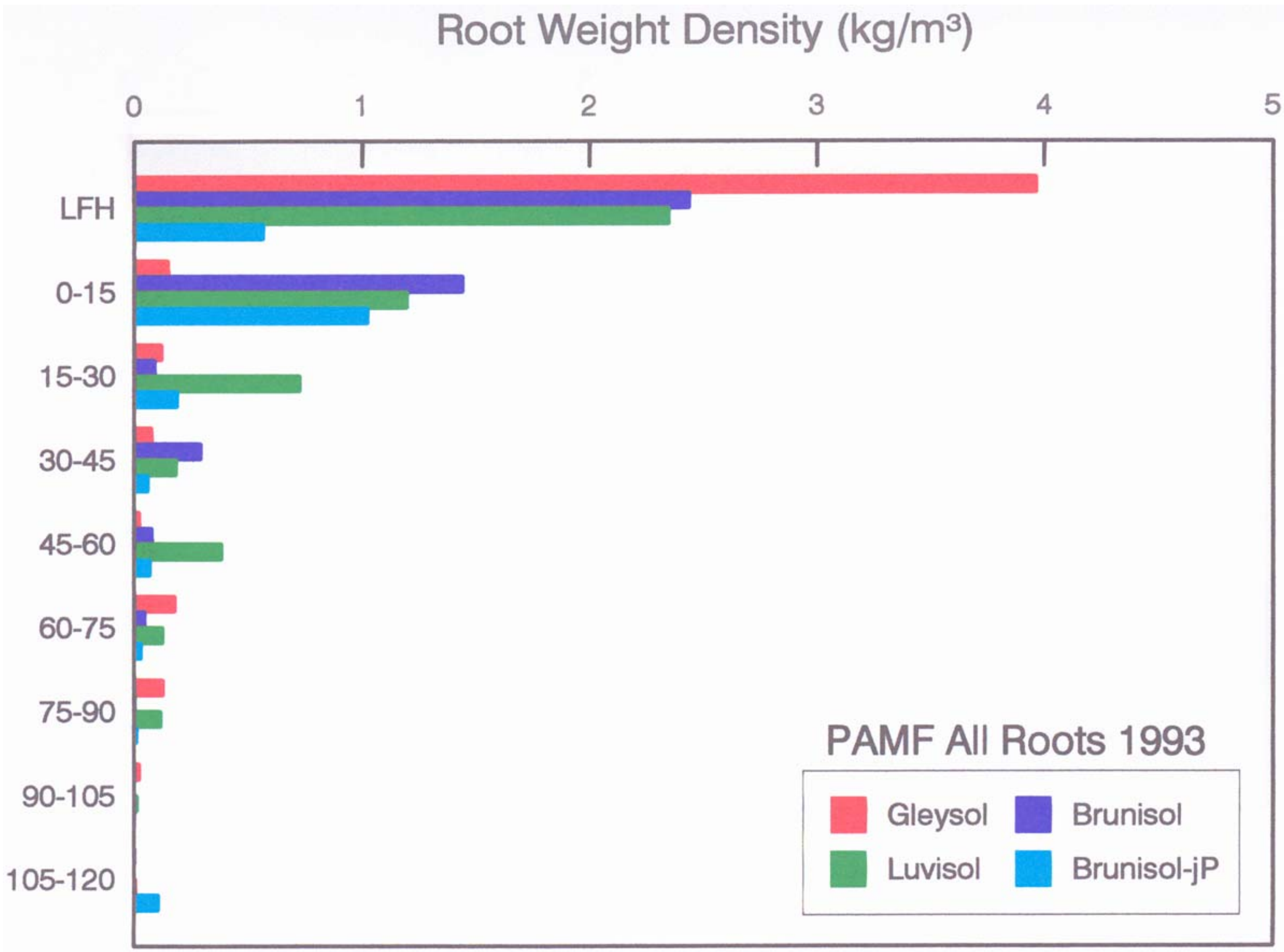

Figure 10.
Root weight density for all species combined for the major soil types.

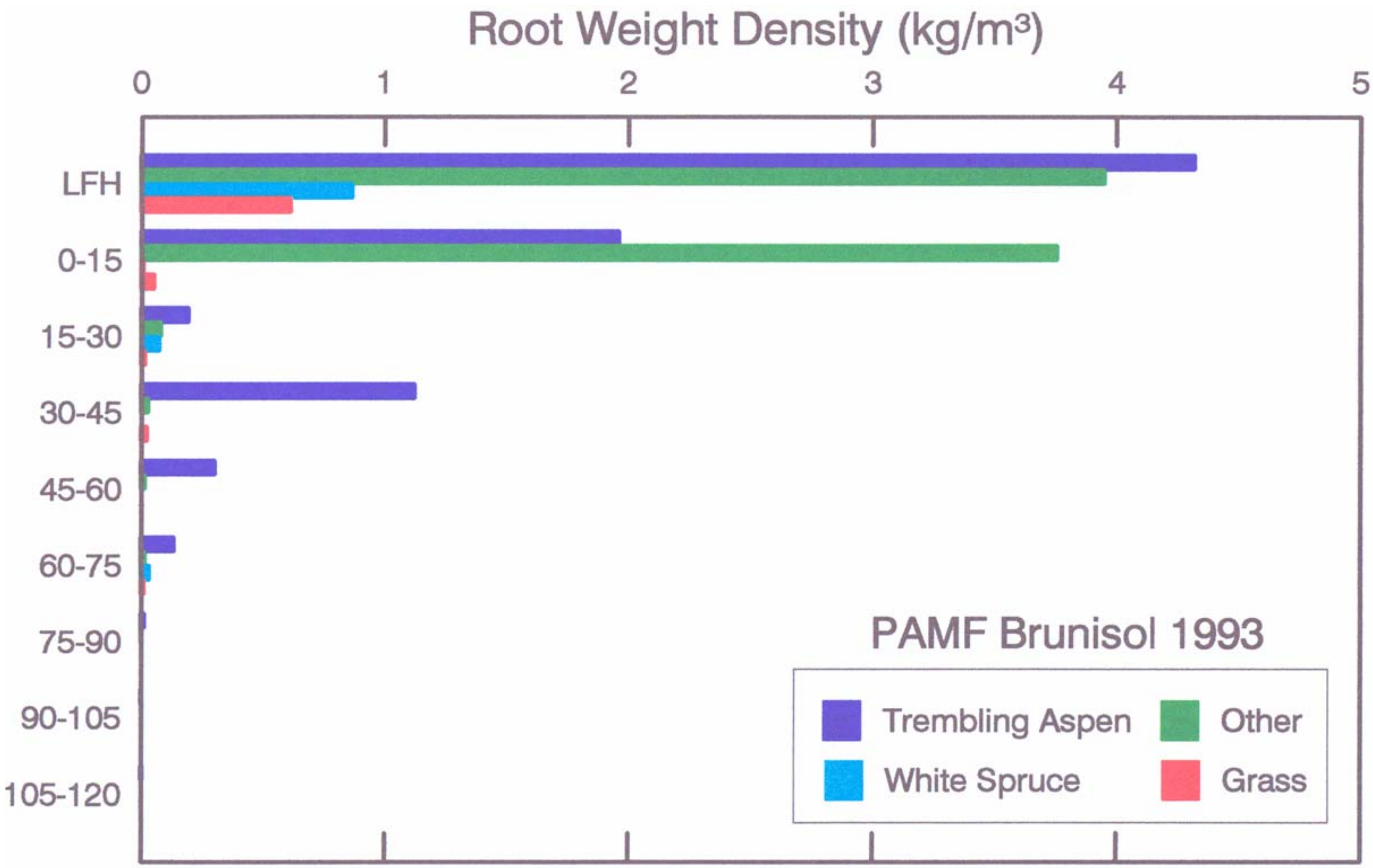

Figure 11.
Root weight density by species for the Mixedwood stand on the Brunisol soil.

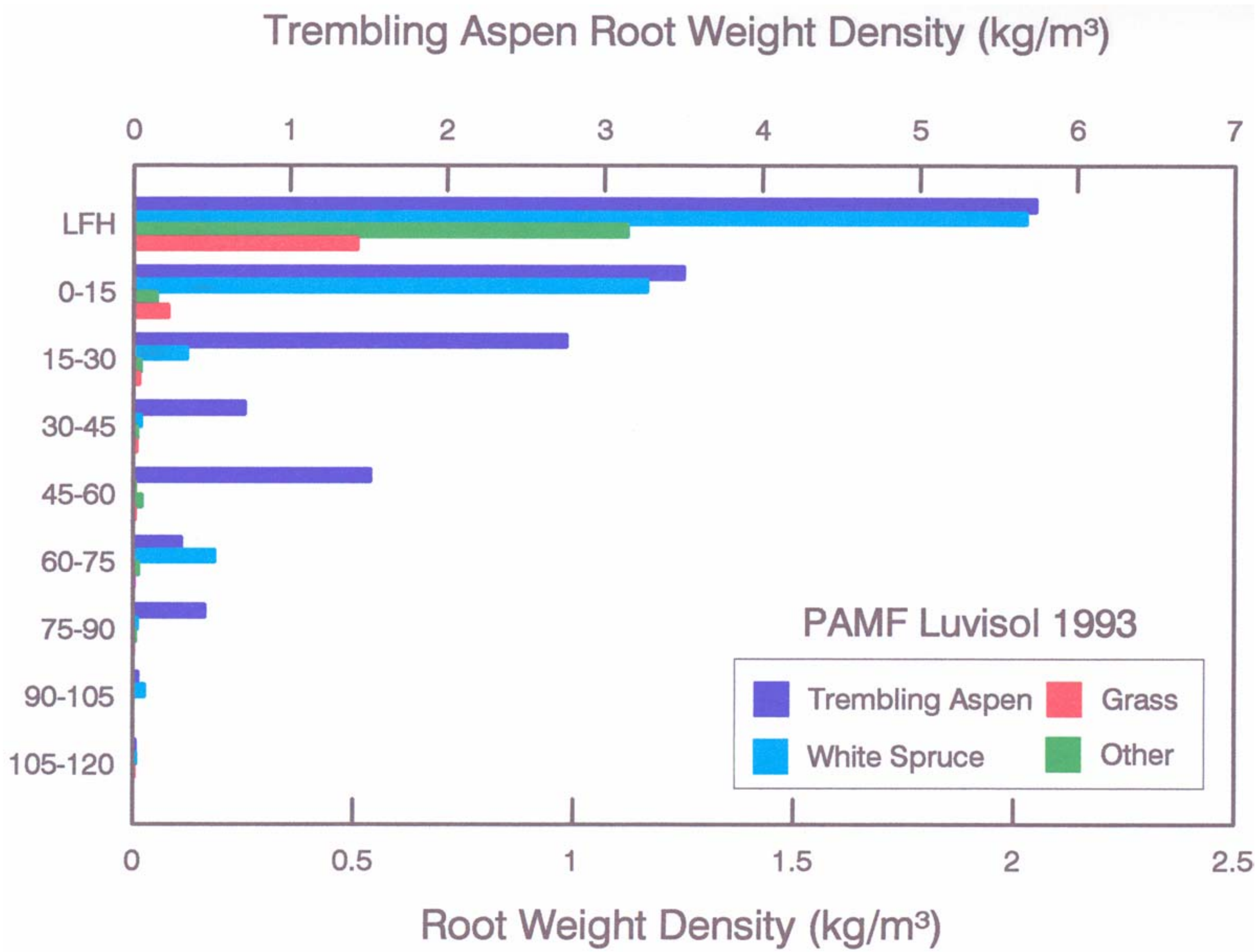

Figure 12.
Root weight density by species for the Mixedwood stand on the Luvisol soil.

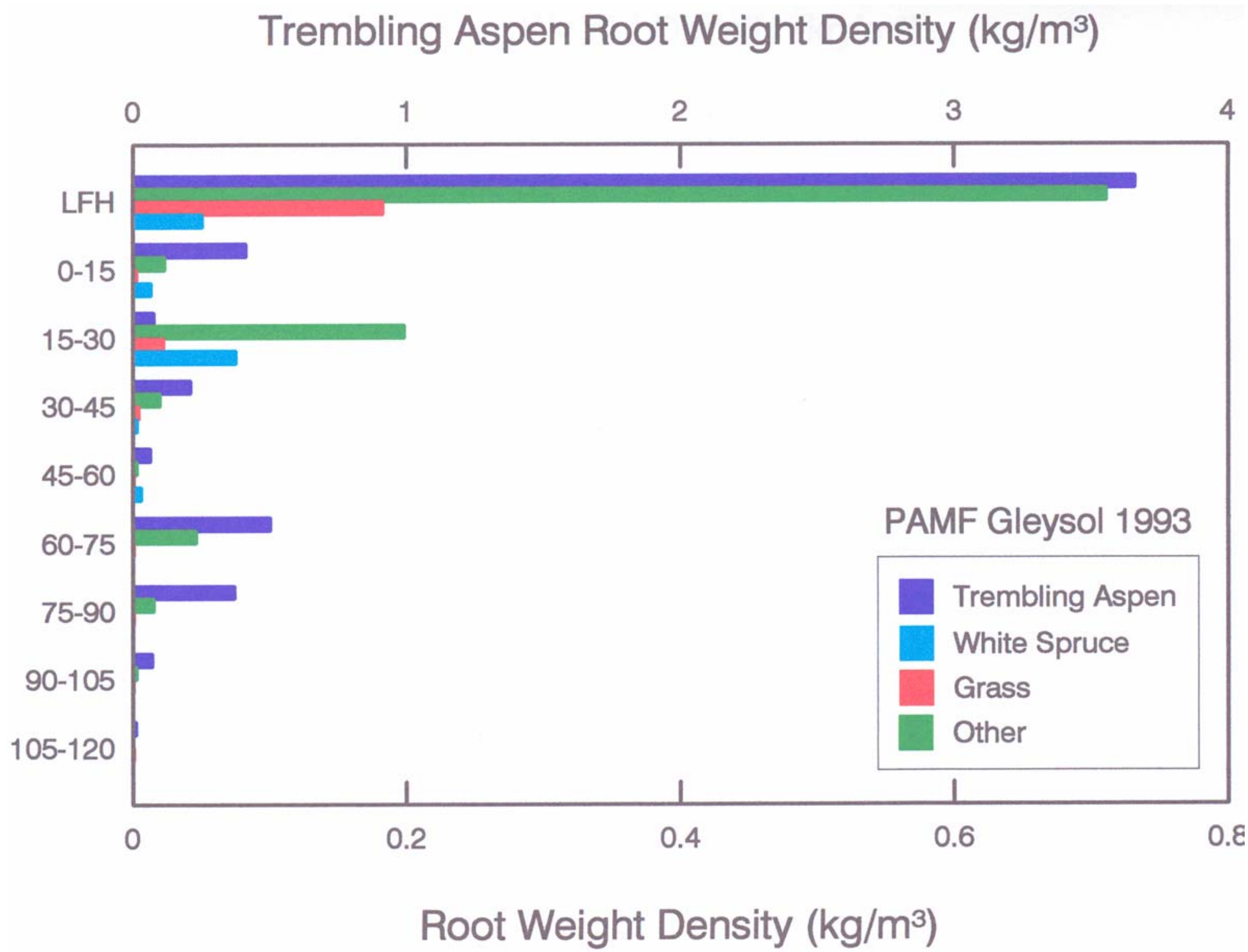

Figure 13.
Root weight density by species for the Mixedwood stand on the Gleysol soil.

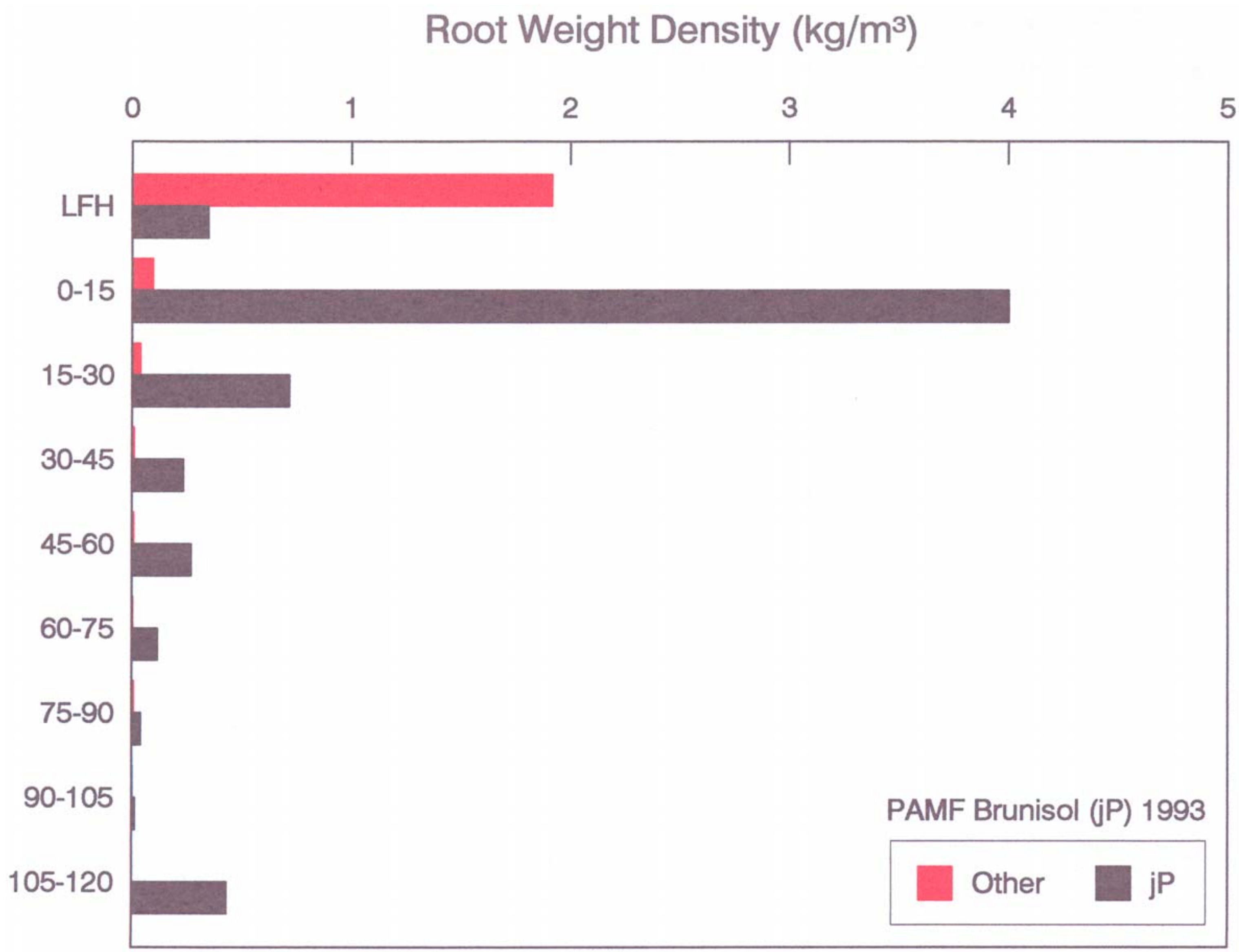

Figure 14.
Root weight density by species for the jack pine growing on the Brunisol soil.

ranged from 0.32 to 29.76 Mg ha^{-1} (avg = 3.0 Mg ha^{-1}) which is lower than the 10.1 Mg ha^{-1} reported by Ruark and Bockheim (1988). White spruce belowground biomass was considerably less than that for aspen and understory species averaging 1.3 Mg ha^{-1}; however, this value compares quite well with the 1.87 Mg ha^{-1} reported by Kimmins and Hawkes (1978) for a mixed stand of old-growth subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and white spruce in British Columbia.

Roots at this site were concentrated in the forest floor except for the jack pine stand. These findings coincide with those reported by Strong and La Roi (1985) for aspen (42-56%), aspen/spruce (46%) and the low concentration in jack pine stands (1 %). Kimmins and Hawkes (1978) also reported that 50% of the subalpine fir/white spruce roots were located in the LFH layer. In Finland, Kalela (1950) found that only 26% and 10% of the spruce and pine roots were located in the LFH. The high concentration of spruce or aspen roots in the forest floor is likely an adaptive strategy by these species since the main source of nutrients, water and warmest soil temperatures are in the forest floor layer. The high concentration of roots in the LFH also suggests the importance of this layer for future tree rotations; hence the removal of this layer during harvesting and silvicultural practices should be minimized. One can speculate that the low nutrient status of the litter layer in the jack pine stand may be a reason for the low concentration of roots in this layer.

Roots of aspen, spruce and pine were found to a 120 cm depth with up to 26% of the aspen root length found below a 60 cm depth. Comerford *et al*. (1984) in a review of subsoil uptake by plant roots concluded that small root densities at depth can play a major role in water and nutrient uptake. Work by Van Rees and Comerford (1986) showed that slash pine roots at a 1 m depth were quite effective in absorbing a tracer especially during the dry season. The importance of aspen, spruce or jack pine roots in subsoils to tree nutrition is intriguing and the significance of these deep roots will require further research.

The number of trembling aspen stems was twice that of white spruce for the study site; however, aspen root length was 10 times higher than that for spruce. This fact would suggest that aspen is a more nutrient demanding species than white spruce and supports the hypothesis of Strong and La Roi (1985) that climax species are less nutrient demanding than seral (aspen) species. However, spruce may have a more efficient mechanism for nutrient absorption and thus may not require a large root surface area. The intent of the 1994-1995 project is to investigate the ability of aspen and spruce roots in different age stands to absorb a tracer to test this hypothesis.

Conclusions

This study is the first to attempt to quantify rooting distributions of both aspen and white spruce trees growing together in a mixedwood stand. Roots of both species and jack pine at another site were found to a depth of 1.2 m. Although there were textural differences between soil types at the research site, root length densities in the mineral soil were very similar with soil depth. Root length densities of aspen were 10 times greater than those of spruce even though the number of aspen stems per ha were only two times greater than spruce. This suggests that either aspen is more nutrient demanding than spruce or spruce roots are more efficient in nutrient uptake. Roots of all species were concentrated in the LFH layer and gradually decreased with depth highlighting the importance of the forest floor in tree nutrition.

References

Bannan, M.W. 1940. The root systems of northern ontario conifers growing in sand. Am. J. Bot. 27:108-114.

Comerford, N.B. G. Kidder and A.V. Mollitor. 1984. Importance of subsoil fertility to forest and non-forest plant nutrition. p. 381-404 In E.L. Stone (ed) Forest Soils and Treatment Impacts, Sixth North American Forest Soils Conference, Knoxville, Tennessee.

Gale, M.R. and D.F. Grigal. 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. For. Res. 17:829-834.

Kabzems, A., A.L. Kosowan, and W.C. Harris. 1988. Mixedwood section in an ecological perspective. Canada-Saskatchewan Forest Resource Development Agreement. Tech. Bull No. 8.

Kalela, E.K. 1950. On the horizontal roots in pine and spruce stand I. Acta Forestalia Fenn. 57:1-79.

Kimmins, J.P. and B.C. Hawkes. 1979. Distribution and chemistry of fine roots in a white spruce - subalpine fir stand in British Columbia: Implications for management. Can. J. For. Res. 8:265-279.

Newman, E.I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139-145.

Ruark, G.A. and J.G. Bockheim. 1987. Below-ground biomass of 10-, 20-, and 32-year-old *Populus tremuloides* in Wisconsin. Pedobiologia 30:207-217.

Schultz, J.D. 1969. The vertical rooting habit in black spruce, white spruce and balsam fir. Ph.D. diss. University of Michigan, Ann Arbor, MI.

Stone, E.L. and P.J. Kalisz. 1991. On the maximum extent of tree roots. For. Ecol. Manag. 46:59-102.

Strong, W.L. and G.H. La Roi. 1983a. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res. 13:577-588.

Strong, W.L. and G.H. La Roi. 1983b. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. 13:1164-1173.

Strong, W.L. and G.H. La Roi. 1985. Root density - soil relationships in selected boreal forests of central Alberta, Canada. For. Ecol. Manag. 12:233-251.

Thomas, R.L., R.W. Sheard and J.R. Moyer. 1967. Comparison of conventional and automated procedures for N, P, and K analysis of plant material using a single digestion. Agron. J. 59:240-243.

Van Rees, K.C.J. and N.B. Comerford. 1986. Vertical root distribution and strontium uptake of a slash pine stand on a Florida Spodosol. Soil Sci. Soc. Am. 50:1042-1046.