ROOT-GROWTH RELATIONSHIPS OF JUVENILE WHITE SPRUCE, ALPINE FIR, AND LODGEPOLE PINE ON THREE SOILS IN THE INTERIOR OF BRITISH COLUMBIA

by S. Eis

Résumé en français

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ABSTRACT

The root systems of 150 white spruce (*Picea glauca* (Moench) Voss), 150 alpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and 75 lodgepole pine (*Pinus contorta* Dougl.), up to 150 cm (5 ft) in height, were excavated. Under restrictive soil conditions, the soil had a controlling effect on the shape of the root system. In deep, permeable soils, owing to the ecotypic variation, the root forms of all species varied from a very shallow to a deep tap root type. For all species, only 7 to 11% of the total root length was greater than .6 mm (.025 inch) in diameter. In relation to tree height, spruce had the greatest lateral root spread, and pine the smallest. The foliage weight was about 3 times greater than the root weight in pine, and twice that in spruce and fir. Pine, at a very young age, used a much greater proportion of carbohydrates for needle growth than spruce or fir. In the juvenile stage it was the most productive species.

RÉSUMÉ

L'auteur déchaussa complètement 150 Épinettes blanches (Picea glauca (Moench) Voss), 150 Sapins Baumiers de l'Ouest (Abies lasiocarpa (Hook.) Nutt.) et 75 Pins Lodgepoles (Pinus contorta Dougl.) mesurant jusqu'à 150 cm (5 pieds) de hauteur. En sols peu propices, la forme générale du système radiculaire était limitée. En sol profond et perméable, vu les variations écotypiques du milieu, les racines des trois espèces d'arbre se développaient en une gamme de réseaux parfois superficiels, parfois munis de racine profondément pivotante. Seulement 7 à 11 pour cent de la longueur totale des racines avaient un diamètre dépassant 0.6 mm (.025 pouce). Par rapport à la hauteur de l'arbre, les racines de l'Épinette s'étendaient le plus, tandis que le Pin avait le réseau le plus restreint. Chez le Pin, le poids du feuillage mesurait trois fois celui des racines, et chez les deux autres genres, ce rapport ne dépassait pas deux. En très bas âge, les Pins utilisaient pour la croissance des aiguilles une beaucoup plus forte proportion d'hydrates de carbone que l'Épinette et le Sapin. A l'état jeune c'était, de plus, l'espèce la plus productive.

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S. Eis¹

INTRODUCTION

The exploitable forests in the interior of British Columbia contain approximately 40,000 million cubic feet of gross volume of usable sound wood. Of this volume 48% is made up of spruces, 18% of pines, 10% of true firs, and 24% of other species (B.C.D.L.F., 1958). Regeneration of these forests after logging or fire is often unsatisfactory.

An earlier study of the germination, survival, and early development of white spruce and alpine fir in the interior spruce forest of British Columbia (Eis, 1965) showed that depth of root penetration and moisture content of the soil were the most important factors affecting establishment and growth. The objective of the present study was to find some of the ecologically significant differences among the three main species of these forests - white spruce, alpine fir, and lodgepole pine that determine their suitability and relative growth on the most frequent forest sites and soils.

MATERIAL

The study was carried out in the Crooked River valley, approximately 30 to 50 miles north of Prince George on two forest sites, Aralia-Dryopteris (good-medium productivity) and Cornus-Moss (medium productivity) (Illingworth and Arlidge, 1960). More than 80% of the spruce forest in the valley occurs on these sites over a variety of soils.

¹Research Scientist, Department of Fisheries and Forestry, Canadian Forestry Service, Forest Research Laboratory, Victoria, British Columbia.

The soils of the study area (Eis, 1965), developed from waterdeposited materials, can be divided into three groups (Figure 1): (1) excessively drained loose sands, deep or underlain by coarse gravelly sands, without lateral seepage; (2) well to moderately drained sandy loams, about 60 cm (24 inches) deep, underlain by sandy clays or compacted till with



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Figure 1. Representative soil profiles. Depth shown is 1 m. (1) Excessively drained loose sands; (2) moderately drained sandy loams; (3) gray sandy clay.

lateral seepage during a part of the growing season; and (3) moderately drained deep lacustrine deposits of gray sandy clay, which are weakly platy when dry and plastic when wet. The thickness of the surface organic material rarely exceeds 5 cm (2 inches) on any soil. In summer, the soil moisture may occasionally go below the wilting point in the top 5 cm (2 inches) for several days (Eis, 1965).

One hundred and fifty white spruce, the same number of alpine fir, and 75 lodgepole pine trees, 1 to 15 years of age and up to 150 cm (5 ft) in height, were examined under a stand as well as in the open. All trees were healthy and had well-developed symmetrical crowns. Since experience had shown that shading plays an important role in growth, trees under different degrees of shade were included. The light intensity affecting each tree was measured during overcast weather with a photoelectric light meter and expressed as a percentage of the full light of adjacent open areas. These measurements are also a rough measure of competition.

Excavations of the entire root systems were done hydraulically with low water pressure to minimize damage to the roots. The length of all recovered roots on representative trees was recorded by diameter classes: .6 mm and below (average .5 mm), .7 to 2 mm (1 mm) and above 2 mm (4 mm); or .025 inch and below (average .02 inch), .03 to .1 inch (.05 inch) and above .1 inch (.2 inch). Stems, branches, needles, and root systems were oven-dried and weighed.

The climate, geology, soils, forest composition, and ground vegetation were described by Kelley and Farstad (1946), Illingworth and Arlidge (1960), and Eis (1965).

RESULTS

General Root Characteristics

All three species, in the early stage of development, had a geotropic radicle that developed into a tap root. Later, as the root system adapted itself to the environment, the lateral roots became more prominent and the tap root frequently became suppressed. A strong tap root usually coincided with an asymmetrical root system or a small number of laterals, as was also found by Rowe (1964) in white spruce.

The distribution of lateral roots around the tree was frequently irregular, and asymmetrical root systems were common. The symmetry of the root system was unrelated to the symmetry of the crown or to topography. Spruce and alpine fir usually had four to six primary lateral roots, while pine had three to five. However, pine developed numerous secondary laterals and, for the same age, pine root systems were denser than those of either spruce or alpine fir. The lateral roots branched at regular intervals over their entire length. The rapid terminal growth of many main lateral roots often lasted only a few years, after which they divided into small roots; and secondary laterals, usually several years younger, became the longest roots of the system. As a result, the density of the root system increased and the ratio of the length of the lateral roots to the tree height decreased. This ratio was largest when the trees were 3 or 4 years of age, amounting to approximately 4:1 in spruce, 3:1 in alpine fir, and 2:1 in pine (Figure 2).

Vertical sinkers were present in all species, regardless of the presence or absence of a tap root. They were most common in lodgepole pine and, as in jack pine (Sims, 1964), they descended from the laterals over a large radius. In spruce, sinkers were usually infrequent and short. In 10-year-old spruce trees, they rarely penetrated more than 20 cm (8 inches) into the soil. The vertical root system of alpine fir was usually restricted to a tap root with sinkers close to the tree; no sinkers occurred under the long laterals. The greater the root competition, the closer to the stump were the sinkers.

Ten-year-old spruce trees had an average total root length of 165 m (540 ft), 14 m (45 ft) (8%) of which was more than .6 mm in diameter, and an average root surface area of 22 dm² (2.4 sq ft) (Table 1). The average weight of needles was 15 g (.42 ounce), which corresponded to 28 dm² (3.0 sq ft) average needle surface area, and was determined by the method of Barker (1968). Pine of the same age had about 2.5 times the average total root length (425 m, 1,400 ft) and more than 4 times the average needle surface area (122 dm², 13.2 sq ft), while alpine fir had about 35% less average root length (108 m, 350 ft) and 10% more average needle surface area (31 dm², 3.4 sq ft). Pine and alpine fir had larger proportions of roots greater than .6 mm (.025 inch) in diameter (about 11%) than spruce. Pine roots were more branched than spruce and had a larger number of very short rootlets along all main roots.

Lodgepole pine, at a very young age, used a much greater proportion of carbohydrates for needle growth than spruce or fir. At 5 years, the needle weight of pine was about 10 times that of spruce and 6 times that of fir.

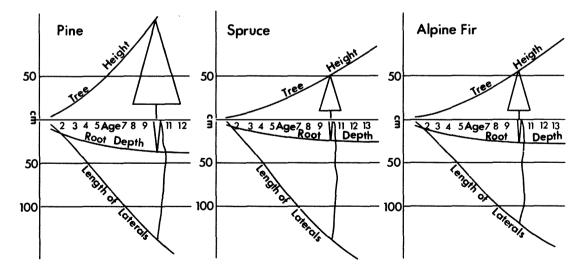


Figure 2. Growth relationships of pine, spruce, and alpine fir.

Table 1. Development of fully exposed seedlings

	Shoot						Needles							
	Aver	age h	eight	Ave	rage wei	ght	Ave	rage wei	ght	Average		ce area		
		CM			<u>g</u>			g			dm ²			
Age	1P	wS	alF	1P	wS	alF	1P	wS	alF	1P	wS	alF		
2	10	5	6	1.1	.11	.14	.7	.06	.09	.9	.2	.2		
4	30	13	14	9.4	.7	1.2	3.8	.4	.7	5	.7	.9		
6	52	23	25	38	3.2	4.7	16.2	1.6	2.9	22	3	4		
8	83	37	34	101	12	18	44	6	9	61	11	12		
10	116	50	53	225	30	48	88	15	23	122	28	31		
12	155	67	75	405	57	84	158	27	45	222	53	61		

(1P - lodgepole pine, wS - white spruce, alF - alpine fir)

Average weight				Rod Average to	ot sys otal ro m	Averag	Average surface area			
Age	1P	wS	alF	1P	wS	alF	1P	wS	alF	
2	.34	.06	.08	8	3	3	2.3	.3	.9	
4	1.6	.2	.4	49	23	18	7	3	3	
6	5.1	1.1	1.5	132	60	40	22	8	7	
8	13.5	3.2	5	262	112	73	40	15	12	
10	28	8	13	425	165	108	76	22	18	
12	50	14	23	575	216	153	115	29	24	

	<u>Shoot weight</u> Root weight			<u>Total root length m</u> Tree height cm			Ratios <u>Needle weight</u> Stem and branch weight			<u>Needle weight</u> Root weight			<u>Needle surface</u> Root surface		
Age	1P	wS	alF	1P	wS	alF	1P	wS	alF	1P	wS	alF	1P	wS	alF
2	3.4	2.0	1.3	82	57	50	1.2	1.3	1.6	1.9	1.1	1.2	.39	.20	.20
4	5.7	2.8	2.5	156	160	120	.8	1.1	1.4	2.7	1.7	1.7	.72	.25	.30
6	7.0	3.3	3.1	250	250	180	.7	1.0	1.2	3.1	1.9	1.9	1.03	.41	.57
8	7.7	3.7	3.6	330	280	200	.7	1.0	1.1	3.2	1.9	1.9	1.35	.76	1.00
10	8.0	3.9	3.7	360	310	205	.7	1.0	1.0	3.2	2.0	1.9	1.65	1.25	1.71
12	8.1	4.0	3.7	370	320	210	.7	1.0	1.0	3.2	2.0	1.9	2.00	1.86	2.50

Effect of Environment - Soils

Where the soils on both forest sites were similar, the root form and the thickness and length of the tap root were similar. Also, no difference in the size of the tap root was found between deep sandy and loamy soils; in both, the root forms of all species varied from a shallow to a deep tap root type, but the proportion that fell into each type varied with species. On clays, the depth of root penetration was usually much less than on permeable soils; the main root system consisted of large laterals forming a flat plate at the level of the incorporated organic material. The tap root was usually weak and short. In shallow sands underlain by coarse gravel, the tap root was frequently distorted, diverted into a horizontal position or branched. Diversion of the tap root did not necessarily reduce the depth of rooting, since oblique penetration by laterals or sinkers often compensated for the lack of a tap root. In general, all species had the greatest root weight, the largest root spread, and the smallest total root length in sands. The small roots were shorter and more branched in humus and loam than those in clay or sand.

On loamy and sandy soils, the average depth and radius of root penetration for each species could be estimated from the size of the stem and the crown (Figure 2). It was impossible, however, to relate the presence or absence of the tap root and sinkers to any above-ground characteristic. On permeable soils for a given tree age, lateral root spread of fully exposed trees was least in alpine fir and greatest in pine; for a given tree height, the ascending order was white spruce, alpine fir, and lodgepole pine. On soils where depth of rooting was restricted, the lateral root spread tended to increase as the rooting depth decreased.

On permeable soils, the tap root system was characteristic of spruce up to 3 years of age. The laterals then became the largest roots and, at 5 to 15 years, 65% of the spruce trees studied had typical shallow root systems that rarely penetrated below 22 cm (9 inches). The remaining 35% developed a distinct tap root that penetrated as much as 38 cm (15 inches). The tap root form was more common in alpine fir and lodgepole pine. Between the ages of 5 and 15 years, a well-developed tap root was found in 55% of the alpine fir (average penetration 26 cm, maximum 45 cm; 10 inches, 18 inches) and in 80% of the lodgepole pine (36 cm, 62 cm; 14 inches, 24 inches). Spruce and fir roots frequently extended just below the surface organic material, while pine roots penetrated deeper into the mineral soil. In all three species, the laterals became more prominent with increase in age and the proportion of trees with a typical tap root system decreased slightly.

In clay soils, there appeared to be a continuous dieback of downward-penetrating roots, and the trees depended entirely on the network of surface roots. Prolonged waterlogging and anaerobic conditions in winter probably caused the death of fine roots that penetrated into the soil when the upper layers were aerated. Day (1963) recorded a similar dying of fine roots on waterlogged soils in winter.

Shading and Root Competition

In this study, a part of the growth response that might appear to be the result of different light intensities under a forest canopy is, in fact, the result of root competition, which normally could not be objectively separated. Where separation was possible, absence of root competition resulted in greater growth and apparent greater shade tolerance.

All three species, up to the age of about 5 years, appeared able to tolerate shade, and reduction of insolation to 50% of the total available did not result in a significant reduction in growth. At 10 years, they required full light and absence of root competition for best growth; 50% insolation reduced growth in pine and spruce significantly (Table 2). Under 25% insolation, pine weighed only 11% of the weight of fully exposed trees, while spruce weighed 21% and alpine fir 45% (Table 2). At least 20% of full light was necessary for satisfactory establishment and growth of lodgepole pine and white spruce, as also stated by Shirley (1945). Alpine fir maintained some growth at light intensities as low as 5%.

			entage of full ociated root c 25%	
		7	%	%
	Height growth	68	35	
Lodgepole	Shoot weight	43	10	
	Needle weight	46	12	Not
pine	Root weight	48	12	
-	Root spread	65	38	alive
	Root depth	48	30	
	Height growth	73	52	
White	Shoot weight	50	19	Not
	Needle weight	53	23	
spruce	Root weight	54	23	alive
•	Root spread	72	55	
	Root depth	57	45	
	Height growth	88	66	30
Alpine	Shoot weight	78	44	12
•	Needle weight	77	53	12
fir	Root weight	78	50	13
	Root spread	90	70	40
	Root depth	75	57	25

Table 2. Dry weight production under reduced light intensities as a percentage of dry weight of seedlings in full light

Competition from deciduous shrubs produced effects similar to but less severe than those resulting from competition from a mature forest. Low herbaceous vegetation appeared to have no significant effect on the growth of seedlings as long as only the roots were in competition and the crowns of seedlings were above the vegetation. Crowding without overtopping by herbaceous vegetation reduced the height growth only slightly, but small diameter increments occurred for several years.

In contrast to results of studies of light effect on seedlings quoted by Kramer and Kozlowski (1960), the greatest decrease in growth due to increased shading and root competition in spruce and pine was in the stem weight, followed by foliage weight and root weight. Shoot to root, stem and branches to root, and needle to root ratios were largest in full light. Lodgepole pine produced proportionally more weight above ground than either spruce or alpine fir. The shoot to root ratio was 3.4:1 at 2 years and 8.0:1 at 10 years in pine, 2.0:1 and 3.9:1 in spruce, and 1.3:1 and 3.7:1 in fir (Table 1).

DISCUSSION

Spruce and alpine fir were usually described as characteristically shallow-rooted (Cheyney, 1942; Place, 1955) and pine as deep-rooted (Kenets, 1932), and the rooting characteristics were considered to be genetically controlled. On permeable soils, different proportions of deepand shallow-rooted individuals in each species suggest genetic control of rooting characteristics, and the variability of root forms on these sites indicates ecotypic variation within the species. In restrictive environmental conditions, certain root forms and adaptabilities are favored (Wagg, 1967). The mechanism controlling the extent to which a species will utilize the forest site is probably the inherent adaptability of the local population to the environment. Absence of pine from white spruce - alpine fir stands on wet spruce sites stems, at least partly, from a greater ecotypic adaptability of spruce and fir to sites where edaphic limitations restrict rooting to surface layers. Further investigation of ecotypic variation within these three species is needed.

In studies in which the effect of light intensity on growth was investigated (e.g. - Shirley, 1945; Logan, 1969), shading reduced the growth of roots more than that of the stem. In this study, the effect of shading cannot be separated from that of root competition. In spruce and pine, the greatest reduction due to shade and competition was in the weight of the stem, followed by foliage weight and root weight. In fir, the order was stem weight, root weight and foliage weight.

All three species attained maximum growth under high light intensities but showed marked differences in their tolerances to low light intensities. Shirley (1945) and Logan (1969) considered growth responses under low light intensities to be an unbiased criterion for assessment of shade tolerance. Shade tolerance cannot be considered as a separate characteristic of a species without consideration of its geographical range and, locally, of its distribution in different habitats. Geographically, a species will be more shade-tolerant in a dry and warm region of its distribution and will occupy different local niches. Locally, a species will grow in a range of habitats; it will show differences in shade tolerance, which are influenced by the moisture regime, and in the ability of the roots to occupy the available soil.

In the central interior of British Columbia, Cornus-Moss sites occur on the ridges and upper slopes of the rolling topography, while Aralia-Dryopteris sites are most common on the lower slopes. Both sites may occur on a range of soils, but the frequency of clay soils is greater on Aralia-Dryopteris than on Cornus-Moss sites. The differences in rooting of the three species were not associated with forest site but rather with the soil texture and the depth of the available soil. Variation in the composition of the tree layer results from the interaction of the soil moisture regime, the shade tolerance, and the rooting habit of the tree species and from the depth of the available soil.

The Cornus-Moss site is dry for fir, medium-dry for spruce, and medium-moist for pine. Pine reproduces only after a disturbance that brings about full light exposure. It is a fast-growing pioneer species with an outstanding ability to occupy the deep permeable soils. Spruce reproduces well in partial shade if moisture is adequate, and seedlings will tolerate shade for many years. Growth is best in full light, though often slow because of frequent drought. Fir is a shade-tolerant species that reproduces and grows well under a canopy of pine or spruce.

The Aralia-Dryopteris site is dry-medium for fir, medium-moist for spruce, and moist-wet for pine. The soil may be saturated in early spring, but the soil surface is usually dry in summer. Pine reproduces only on humps, in full light, and is generally infrequent. Spruce can tolerate some shade but grows well only in full light. The Aralia-Dryopteris site is a true medium-quality spruce habitat. Fir forms an understory in a mature stand; it regenerates and persists under moderate shade, but the best growth is under light shade or full light exposure.

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