PATTERNS OF VARIATION IN ROOT SYSTEMS OF SCOTCH PINE PROVENANCES

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ABSTRACT

PATTERNS OF VARIATION IN ROOT SYSTEMS OF SCOTCH PINE PROVENANCES

by James H. Brown

Root development of nursery and greenhouse grown seedlings of Scotch pine (*Pinus sylvestris* L.) provenances from throughout the range of the species was studied. Significant differences were found between origins in type of root system, rate of growth, root regeneration potential and growth at different moisture-fertility combinations.

Root systems of 45 origins that had been grown in the greenhouse for periods of four and eight months were analyzed. Northern origins were distinctly tap-rooted, with lateral rooting confined to branching from upper portions of the tap root. Root length was well correlated with average annual temperature of the area of seed collection. Central European provenances had more moderate expression of the tap root character. Laterals were long, much branched, and occurred along most of the tap root. Differences in root characteristics could not be correlated with climate.

Sources from isolated, southern portions of the range were distinctly tap-rooted. Branching of laterals was low. There was considerable variation in other characters and individual root types apparently developed in response to differences in precipitation and past evolutionary history. Provenances from southern France had root types similar to those of northern origins. Lateral rooting was

confined to branching from upper portions of the tap root. Root systems of Spanish origins had a narrow, columnar appearance. Tap roots were long and laterals were short and extended from along most of the tap root. Greek origins from cool, moist climates had root types intermediate between those of other southern origins and those of central European sources. Provenances from Turkey and the Georgian SSR were deeply tap-rooted and individual laterals were longer than on Spanish provenances.

Rates of root growth during the first 80 days after germination were studied for greenhouse grown seedlings of eight origins. Differences were related to temperature and precipitation of areas of seed collection. Initial root growth was confined to tap root elongation. Lateral growth was not pronounced until after tap root growth began to decline. Rate of root growth was most rapid for northern sources from areas having short growing seasons and was slowest for southern origins from moist climates.

Five nursery grown provenances were transplanted at monthly intervals during the first growing season and survival, root growth and root regeneration were studied. Results varied with time of transplanting, seed source and intensity of root pruning. Survival was closely correlated with amount of roots present at transplanting and growth of new roots after transplanting. Root growth and root regeneration were slight while top growth was active. Survival of trees transplanted during this period was very low. Root growth and regeneration increased significantly after top growth stopped. Survival was nearly 100 percent for trees transplanted after this time. Variations in seasonal patterns of root growth and survival were correlated with growth patterns of origins used.

There were differences between provenances in root regeneration potential. It was highest for south-Swedish, south-French and Spanish origins and lowest for north-Swedish and German sources. Intensity of root pruning also affected survival and root regeneration. Survival was lowest for fully root-pruned trees and approximately the same for no and half root-pruned trees. Trees with half root pruning produced the greatest amount of new roots after transplanting.

Three provenances were grown in the greenhouse for 90 days under different moisture-fertility treatment combinations. There were differences between origins in optimums for growth and in requirements for shoot and root growth. Sources from Germany and Sweden showed similar reactions to different treatment combinations. The Spanish origin reacted differently and had lower fertility and higher moisture requirements. Fertility levels for best root growth were lower than those for best shoot growth.

PATTERNS OF VARIATION IN

ROOT SYSTEMS OF SCOTCH PINE PROVENANCES

By

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CHAPTER I

INTRODUCTION

Scotch pine (Pinus sylvestris L.) is native over a wide geographic area in Europe and Asia. Its range reaches from above the Arctic Circle in northern Scandinavia to Spain and Turkey in the south and from Scotland in the west to northeastern Siberia near the Pacific Ocean in the east. In southern and western Europe the range is discontinuous. In other areas it is generally continuous over large areas (Figure 1). Scotch pine has also been introduced extensively outside its native range. It is now the most commonly planted species for Christmas tree use in the United States. Many trees are also planted for reclamation, stabilization and wood production.

Within its natural range Scotch pine shows wide variability. This variation has been the subject of a number of provenance studies (reviewed by Wright and Bull, 1963 and Ruby, 1964). Ruby (1964) recognized at least 21 geographic varieties of the species.

In the late 1950's an intensive provenance study of Scotch pine was initiated at Michigan State University as part of the NC-51 project, "Forest Tree Improvement through Selection and Breeding." With the cooperation of researchers and seed dealers in Europe, lots of Scotch pine seed were collected from 186 stands throughout the range of the species. These were sown in the Bogue Forest Research Nursery on the Michigan State University campus in the springs of 1959 and 1961. Five replicates were used. The first four of these comprised a randomized complete block experimental design. These were used to study characteristics of seedlings of different origin in

the nursery. Results of this study were published by Wright and Bull in 1963. The fifth replicate provided seedlings for field plantations. These replicated plantings were made at 33 permanent locations in eight north central states, plus New York and Maryland. Initial results from these plantings were reported by Wright et al. in 1966.

Measurements made in the nursery and outplantings revealed significant differences between provenances in a number of shoot characteristics. These generally showed definite geographic trends. In most instances there was little interaction between seedlot and location of test plantation, despite the wide variety of sites on which plantations were established (King, 1965a and 1965b; Wright et al., 1966).

When seedlings were lifted from the nursery for outplanting there seemed to be distinct differences in root types. These also appeared to exhibit geographic trends, although this was not substantiated by detailed studies. In general, southern origins appeared to be more tap-rooted than those from further north. In lifting half or more of the tap root and most of the lateral roots were often lost on southern origins. On more northerly origins less of the root system was damaged or lost in lifting. In subsequent outplantings, however, there was no apparent correlation between damage to root systems during lifting and survival. It was generally best for southern provenances and poorest for northern ones.

CHAPTER II

OBJECTIVES

The general objective of the studies reported here was to investigate variations in root types of different geographic origins of Scotch pine in an effort to help explain differences in top growth and survival after outplanting. Specific objectives were:

(1) To classify the root systems of Scotch pine provenances and to relate differences to the climate of place of origin.

(2) To study the pattern of root development of different Scotch pine origins for the first twelve weeks after seed germination and to relate these patterns to differences in the climate of place of origin.

(3) To determine the survival, root growth and root regeneration potential of Scotch pine of different origins when transplanted at different times of the year.

(4) To study the growth of Scotch pine from widely separated portions of the species range when grown at varying moisture and fertility levels.

CHAPTER III

VARIATION IN ROOTS OF GREENHOUSE GROWN SEEDLINGS OF DIFFERENT SCOTCH PINE PROVENANCES

There have been numerous studies of variations in root systems of different tree species. Toumey (1929) classified the root types of tree species into two general groups: those with tap roots which grew rapidly downward and penetrated deeply; and those with slowly growing primary roots and extensive, rapidly growing lateral roots. Holch (1931), found that each of the several species of tree seedlings which he studied had its own characteristic root type.

Studies have shown pronounced differences in root types of various conifer species. These include investigations of Corsican pine (Aldrich-Blake, 1930), Douglas-fir (McMinn, 1963), jack pine (Cheney, 1932; Day, 1945, Kaufman, 1945), loblolly pine (Gruschow, 1959), lodgepole pine (Preston, 1942), longleaf pine (Heyward, 1933; Lennart, 1934; Pessin, 1935), pitch pine (McQuilken, 1935), ponderosa pine (Curtis, 1964), red pine (Day, 1941), shortleaf pine (Turner, 1936; Reed, 1939), and white pine (Stevens, 1931).

There has been only limited study, however, of racial variation in the root systems of forest tree species. Snyder (1961) found that roots of longleaf pine from southeastern Georgia appeared to be more fibrous than those of seedlings from farther west in the range of the species. He theorized that the more fibrous root types had evolved in response to wetter summers and falls which prevail in the eastern part of the species range. Leibundgut and Dafis (1962) observed differences in root types and extents of four provenances of European larch. Some differences have also been noted for Scotch pine. Laitakari (1929) excavated roots in native Scotch pine stands in central and southern Finland and found differences in both type and extent of root systems. The study of Leibundgut and Dafis (1964) with four central European provenances showed variations in dry weights and diameter distribution of roots. Bibleriether (1964) worked with a number of German provenances of Scotch pine which had been planted in 1936 and found that tap roots of sources from the East Prussian area were more clearly defined, deeper and less branched than those of provenances from west-central Germany.

PROCEDURE

For this study 45 seed sources of Scotch pine were selected from throughout the range of the species. The seed was originally collected for a provenance study conducted by Wright and Bull (1963). Each seedlot was gathered by cooperators in Europe and Asia from ten or more average trees in stands of several acres (Table 1, Figure 1). The climatic data were compiled by John L. Ruby (1964) and are from weather stations located as closely as possible to the stands from which the seeds were collected. In most cases the data apply to the area of collection; in a few cases to stations some miles from locations of collection. An "Index of Aridity" was calculated using De-Martonne's (1926) formula: $\text{Index} = \dfrac{\text{precipitation in mm.}}{\text{temp. in } ^{\circ}\text{C.} + 10}$. The smaller the index value, the drier the climate.

Seedlings were grown in the greenhouse for periods of four and eight months using a randomized complete block design with four replications and two trees (containers) per plot. Seed was sown in January 1965 in individual containers, with five seed per container. The containers were approximately 8 inches deep and 4 inches square. Germination began nine days after sowing and was completed eight days later. Two weeks after germination the seedlings were thinned to one per container. The potting mixture consisted of one-third (by volume) each of builders sand, peat moss, and a sandy loam nursery soil. A complete fertilizer had been added to the mixture to give the equivalent of approximately 50 ppm each of N, P_2O_5, and K_2O. This coarse, porous mixture permitted unrestricted rooting and recovery of the root systems with a minimum of damage.

The seedlings were watered at intervals to keep the moisture

Table 1. Location and climate at place of origin of Scotch pine provenances used in the study of differences in root types.

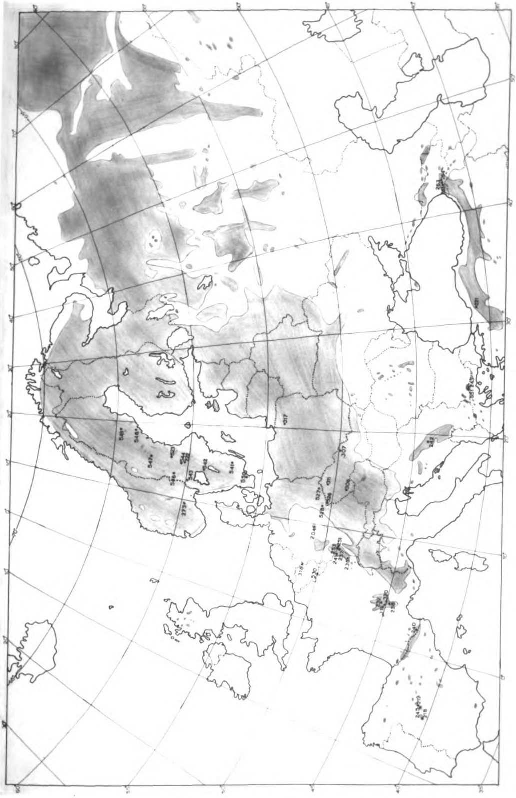
MSFG No., Country (a)	Lat. N	Long. E	Elev.	Temperature Annual	Temperature April-Sept.	Precipitation Annual	Precipitation April-Sept.	Index of Aridity (b) Annual	Index of Aridity (b) April-Sept.
	°	°	feet	°C	°C	millimeters		number	
var. mongolica									
254 SIB	60.8	131.6	2500	-11.6	8.1	188	145	188+	8.0
255 SIB	52.4	117.7	2000	3.3	11.3	377	342	28.4	16.1
var. lapponica									
549 SWE	64.5	18.7	800	0.6	8.0	493	310	46.7	17.2
548 SWE	63.5	18.7	700	2.0	8.5	568	299	47.3	16.2
547 SWE	62.5	15.7	700	2.9	9.1	525	332	40.7	17.4
546 SWE	60.9	13.4	1500	1.2	8.6	617	383	55.1	20.6
var. septentrionalis									
523 SWE	61.3	16.0	700	4.8	11.3	557	354	37.6	16.6
544 SWE	60.4	14.9	800	6.2	12.6	630	347	38.9	15.4
222 SWE	60.2	15.0	800	4.8	11.3	557	354	37.6	16.6
543 SWE	59.9	12.0	700	6.2	12.6	630	347	38.9	15.4
273 SWE	59.7	9.5	600	3.2	10.0	811	482	61.4	24.1
var. rigensis									
542 SWE	58.8	14.3	400	6.2	12.6	630	347	38.9	15.4
541 SWE	57.0	15.6	500	6.2	11.8	533	334	32.9	15.3
550 SWE	55.9	14.1	100	6.9	12.0	468	266	27.7	12.1
var. altaica									
256 SIB	56.7	96.3	1300	1.8	9.3	249	191	21.1	9.9
234 SIB	56.0	95.0	600	1.8	9.3	249	191	21.1	9.9
var. polonica									
317 POL	53.7	20.5	500	7.1	13.6	568	372	33.2	15.8
var. hercynica									
204 GER	50.8	9.7	1300	8.6	14.1	592	337	31.8	14.0
527 GER	50.8	13.7	1800	7.5	13.1	746	429	42.6	18.6
528 GER	50.6	12.0	1500	7.7	13.4	608	388	34.4	16.6
311 CZE	50.5	14.7	1000	9.0	15.6	490	335	25.8	13.1
526 GER	50.4	12.2	1700	6.2	11.9	762	444	47.0	20.3
307 CZE	49.9	17.9	800	8.8	15.5	630	407	33.5	16.0
306 CZE	49.2	14.0	1500	8.2	14.1	606	424	33.3	17.6
var. haguenensis									
318 BEL (c)	51.2	5.5	--	9.3	13.8	825	416	42.7	17.5
530 BEL (c)	50.0	5.0	--	7.4	11.9	1251	570	71.9	26.0
241 FRA	49.1	7.4	800	9.2	14.7	734	384	38.2	15.5
251 GER	49.1	8.1	500	9.9	15.5	536	305	26.9	12.0
253 GER	49.1	7.8	1300	9.5	15.0	612	338	31.4	13.5
237 FRA	48.8	7.8	500	9.8	15.7	777	441	39.2	17.2
var. illyrica									
242 YUG	43.9	19.4	1300	9.5	16.0	791	441	40.6	17.0
var. rhodopaea									
243 GRE	41.5	24.2	5600	7.4	12.7	2460	1190	141.4	52.4
551 GRE	41.3	23.4	5000	7.4	12.7	2460	1190	141.4	52.4
var. armena									
221 TUR	40.5	32.7	5000	11.6	17.7	345	147	16.0	5.3
263 GEO	41.8	43.4	3400	12.2	19.1	533	357	24.0	12.3
264 GEO	41.7	43.5	4900	12.2	19.1	533	357	24.0	12.3
261 GEO	41.6	42.6	3400	12.2	19.1	533	357	24.0	12.3
var. aquitana									
235 FRA	48.2	7.2	2200	8.9	14.5	1372	699	72.6	28.5
239 FRA	45.3	3.7	3100	9.0	13.9	780	503	41.1	21.0
316 FRA	45.1	3.5	3200	9.0	13.9	780	503	41.1	21.0
320 FRA	45.0	4.0	3000	9.0	13.9	780	503	41.1	21.0
238 FRA	44.7	3.8	2900	9.0	13.9	858	445	45.2	18.6
240 FRA	42.6	2.1	4700	5.9	9.9	799	412	50.3	20.7
var. iberica									
245 SPA	40.7	-4.2	4900	11.9	17.5	508	264	23.2	9.6
218 SPA	40.0	-5.3	3700	10.0	15.3	366	174	18.3	6.9

(a) The numbers are those used in the Michigan State Forest Genetic accession record. The countries are BELgium, CZEchoslovakia, FRAnce, GEOrgian SSR, GERmany, GREece, NORway, SIBeria, SPAin, SWEden, TURkey, YUGoslavia.

(b) Index of aridity = $\frac{\text{Precipitation in millimeters}}{\text{Temperature in } ^{\circ}\text{C.} + 10}$

(c) Seed obtained from plantation.

Figure 1. Natural distribution of Scotch pine (shaded) and provenances included (numbered dots) in the study of differences in root types. In addition to those provenances shown, four additional sources from the eastern portion of the range (MSFG 234, 254, 255, 256) were also used.



level near field capacity. At the end of the growing periods, containers were taken from the greenhouse, dumped and the root systems carefully washed. The trees were measured immediately.

All analyses of variance were conducted by using means of the 2-tree plots as items. Provenance means were used as items in correlation calculations.

RESULTS

The data were grouped by the geographic varieties proposed by Ruby (1964). The patterns of root development generally followed Ruby's varietal patterns based on seed and 2-year growth characteristics and 5- to 7-year growth in NC-51 plantations (Wright et al., 1966). Departures from Ruby's groupings are discussed whenever appropriate. Summaries of analyses of variance are given in Table 2.

Results obtained at four and eight months were similar. Correlation coefficients between measurements made at the end of the two sampling periods ranged from 0.856 for tap root lengths to 0.988 for height (significant at 1 percent level with 43 d. f.). In general the amount of growth during the second four-month period was considerably less than during the first four-month period (Tables 3,4,5). Top growth, in terms of both length and weight, was very slight, ranging from 0 to approximately 15 percent. Tap root growth was also relatively slight, the second four-month increase in length varying from 6 to 22 percent; in weight from 0 to 30 percent. Lateral growth during the second four-month period was greater; increases in length varied from 10 to 70 percent and increases in weight from 25 to 75 percent. The percentage increase between the fourth and eighth month was not correlated with location or climate at place or origin (Table 1).

There were decided differences in root characteristics of seedlings from different origins. Many were adaptive characters which could be correlated with environmental conditions in the areas from which seed was collected. Some could not be correlated. Seedlings of all provenances were tap-rooted. The degree to which this

Table 2. Summary of analyses of variance for top and root growth factors studied in sampling Scotch pine provenances after four and eight months growth in the greenhouse.

Factor	F ratios for sampling at	
	Four Months	Eight Months
Top Length	7.02***	27.25***
Tap Root Length	14.22***	18.08***
Lateral Root Length	8.92***	13.40***
Top Weight	20.33***	23.24***
Tap Root Weight	46.66***	59.33***
Lateral Root Weight	8.62***	14.54***
Tap Root Weight/Unit Length	22.19***	27.18***
Top Length / Total Root Length	3.51***	9.59***
Top Weight / Total Root Weight	4.20***	5.99***
Total Lateral Root Length / Taproot Length	4.25***	5.61***
Longest Lateral Root Length / Taproot Length	5.59***	4.66***
Lateral Root Weight / Taproot Weight	6.10***	10.25***
No.: Total Lateral Roots	9.28***	15.68***
No.: Lateral Roots, Unbranched	9.15***	15.46***
No.: Lateral Roots, 1 branch	8.68***	10.38***
No.: Lateral Roots, 2 branches	9.72***	10.90***
No.: Lateral Roots, 3 branches	5.98***	11.42***
No.: Lateral Roots, 4 branches	None	2.85***

(a) With 44 degrees of freedom in treatment (seed source) mean square and 132 degrees of freedom for error mean square.

*** Significant at 0.1 percent level.

Table 3. Shoot and root development of Scotch pine provenances grown four months in the greenhouse.

MSFO No., Country of Origin	Length of Shoot	Length of Tap Root	Length of Lat. Root	Weight of Shoot	Weight of Tap Root	Weight of Lat. Root	Tap Root Wt./ Unit Length	Top-Root Ratios: Top Length / Tot. Rt. Length	Top-Root Ratios: Top Weight / Tot. Rt. Weight	Root Ratios, Length: Total Lateral / Taproot	Root Ratios, Length: Longest Lateral / Taproot	Root Ratios, Weight: Lateral Root / Taproot
	mm.	cm.	cm.	---milligrams---			mg./cm.	-----number------		----------number---------		
var. mongolica												
254 SIB	34	13	80	24	7	16	.53	.036	1.03	6.1	1.16	2.3
255 SIB	40	22	112	40	10	25	.46	.029	1.15	5.0	.74	2.4
var. lapponica												
549 SWE	30	18	89	16	7	15	.38	.029	.75	5.0	.70	2.4
548 SWE	41	19	124	25	7	22	.35	.028	.88	6.5	.90	3.3
547 SWE	40	20	116	25	8	24	.43	.030	.78	6.0	.80	2.9
546 SWE	37	19	92	24	7	20	.38	.033	.89	4.9	.67	2.8
var. setentrionalis												
523 SWE	41	22	126	31	10	27	.43	.029	.87	5.6	.73	2.7
544 SWE	45	23	127	28	12	29	.52	.031	.94	5.4	.81	2.4
222 SWE	43	21	115	30	9	32	.43	.032	.93	5.4	.63	2.6
543 SWE	42	21	117	32	11	33	.51	.030	.95	5.4	.77	2.2
273 NOR	35	22	99	27	12	22	.51	.029	.80	4.4	.79	1.9
var. rigensis												
542 SWE	42	22	117	32	9	25	.41	.030	.94	5.3	.80	2.9
541 SWE	43	21	133	31	9	25	.42	.028	.78	6.3	.95	2.8
550 SWE	44	24	142	37	12	28	.51	.027	.93	5.9	.83	2.3
var. altaica												
256 SIB	42	24	159	39	11	34	.45	.023	.86	6.6	.78	3.2
234 SIB	43	24	150	37	9	38	.39	.025	.79	6.3	.89	4.2
var. polonica												
317 POL	48	24	187	55	14	40	.57	.023	1.02	7.6	1.00	2.9
var. hercynica												
204 GER	47	24	156	49	14	36	.57	.026	.99	6.6	.78	2.6
527 GER	47	24	161	42	12	32	.49	.026	.96	6.8	.84	2.9
528 GER	49	27	161	44	12	31	.43	.027	1.04	5.9	.64	2.6
311 CZE	46	26	144	44	11	29	.44	.028	1.11	5.6	.68	2.5
526 GER	44	22	141	41	11	29	.49	.027	1.04	6.3	.78	2.6
307 CZE	48	26	158	40	12	29	.47	.026	.97	6.1	.79	2.4
306 CZE	44	26	140	43	12	28	.46	.027	1.08	5.4	.53	2.3
var. haguenensis												
318 BEL	49	25	173	48	13	36	.53	.025	1.00	7.1	.89	2.7
530 BEL	55	30	276	79	17	56	.56	.018	1.09	9.4	.90	3.4
241 FRA	51	32	222	54	13	39	.45	.020	1.01	6.9	.59	2.7
251 GER	51	24	179	58	12	32	.48	.025	1.34	7.5	1.02	2.9
253 GER	54	25	230	59	14	51	.58	.021	.91	9.3	.94	3.6
237 FRA	53	25	192	43	14	27	.54	.024	1.09	7.9	.81	2.0
var. illyrica												
242 YUO	49	23	187	59	18	51	.79	.024	.86	8.2	.95	2.8
var. rhodopaea												
243 GRE	49	27	201	67	16	42	.60	.022	1.20	7.4	.99	2.6
551 GRE	50	26	162	59	16	34	.60	.026	1.20	6.3	.97	2.2
var. armena												
221 TUR	47	30	166	65	21	43	.72	.026	1.02	5.4	.72	2.0
263 GEO	48	28	159	61	21	42	.73	.026	.99	5.6	.56	2.0
264 GEO	49	26	198	78	23	59	.90	.022	.96	7.8	1.00	2.6
261 GEO	47	25	147	67	20	38	.82	.027	1.16	6.1	.79	1.9
var. aquitana												
235 FRA	44	25	148	43	12	29	.50	.026	1.05	6.0	.91	2.4
239 FRA	44	24	164	58	17	40	.70	.024	1.03	6.9	.99	2.4
316 FRA	43	25	157	49	15	35	.61	.026	.99	6.2	.77	2.3
320 FRA	44	23	140	49	17	28	.72	.027	1.10	6.0	.71	1.7
238 FRA	42	23	141	50	16	37	.71	.025	.94	6.2	.85	2.3
240 FRA	42	25	130	45	22	29	.89	.027	.87	5.2	.85	1.3
var. iberica												
245 SPA	50	36	168	80	41	43	1.32	.025	.88	4.7	.36	.9
218 SPA	52	42	174	89	45	48	1.09	.024	.95	4.2	.27	1.0
$LSD_{.10}$	3.1	2.8	29	9	2.7	8	.03	.002	.14	1.3	.16	.55
$LSD_{.05}$	3.7	3.3	35	10	3.3	9	.04	.003	.16	1.5	.20	.66
$LSD_{.01}$	4.9	4.4	47	14	4.3	12	.05	.004	.22	2.0	.26	.87

Table 4. Shoot and root development of Scotch pine provenances grown eight months in the greenhouse.

NSFO No., Country of Origin	Length of Shoot	Length of Tap Root	Length of Lat. Root	Weight of Shoot	Weight of Tap Root	Weight of Lat. Root	Root Wt./Unit Length	Top-Root Ratios: Top Length / Tot. Rt. Length	Top-Root Ratios: Top Weight / Tot. Rt. Weight	Root Ratios, Length: Total Lateral / Taproot	Root Ratios, Length: Longest Lateral / Taproot	Root Ratios, Weight: Lateral Root / Taproot
	mm.	cm.	cm.	milligrams	milligrams	milligrams	mg./cm.	number	number	number	number	number
var. mongolica												
254 SIB	32	15	90	25	8	22	.50	.020	.86	5.8	1.16	2.9
255 SIB	40	24	119	41	11	29	.45	.028	1.02	4.9	.86	2.7
var. lapponica												
549 SWE	32	20	105	18	9	22	.48	.026	.58	5.4	.75	2.3
548 SWE	40	21	134	26	8	31	.39	.026	.66	6.4	1.02	3.9
547 SWE	42	21	172	26	10	40	.46	.022	.53	8.3	1.05	4.2
546 SWE	40	20	118	33	7	28	.36	.029	.96	6.0	1.03	3.9
var. septentrionalis												
523 SWE	41	25	158	34	10	35	.41	.023	.75	6.4	.90	3.7
544 SWE	45	25	180	38	13	41	.55	.023	.72	7.2	1.03	3.1
222 SWE	43	22	171	35	10	42	.46	.023	.68	7.8	1.01	4.1
543 SWE	43	26	187	34	14	35	.54	.021	.68	7.2	1.05	2.6
273 NOR	38	25	156	30	13	31	.51	.021	.70	6.3	.97	2.4
var. rigensis												
542 SWE	39	27	175	34	14	46	.48	.020	.58	6.8	.92	3.7
541 SWE	42	24	175	33	11	36	.46	.022	.70	7.2	.88	3.3
550 SWE	47	28	195	41	12	49	.45	.021	.68	7.2	.99	4.1
var. altaica												
256 SIB	44	25	206	43	12	49	.47	.019	.72	8.1	1.07	4.2
234 SIB	43	26	191	41	9	43	.34	.031	.81	7.4	.87	4.9
var. polonica												
317 POL	50	27	268	58	14	61	.53	.018	.78	9.8	1.08	4.2
var. hercynica												
204 GER	49	28	202	52	14	44	.59	.022	.87	7.3	1.04	2.7
527 GER	49	28	247	47	15	56	.53	.018	.66	8.8	1.08	3.7
528 GER	52	28	265	47	13	59	.45	.018	.66	9.3	.95	4.6
311 CZE	49	28	234	46	12	62	.43	.019	.62	8.4	1.01	5.1
526 GER	48	26	242	53	15	52	.56	.018	.81	9.3	1.16	3.7
307 CZE	50	26	195	45	13	36	.49	.023	.95	7.4	.83	2.8
306 CZE	48	27	198	43	11	38	.44	.021	.89	7.3	.81	3.2
var. haguenensis												
318 BEL	54	27	308	57	15	60	.56	.016	.75	11.6	1.10	4.0
530 BEL	58	31	364	82	18	81	.60	.015	.82	11.6	1.09	4.4
241 FRA	53	32	312	47	14	67	.45	.015	.60	9.8	.88	4.5
251 GER	54	29	296	64	14	68	.50	.017	.78	10.2	1.16	4.7
253 GER	53	26	328	60	16	70	.60	.015	.70	12.6	1.26	4.5
237 FRA	57	26	276	47	15	47	.57	.020	.78	10.3	1.04	3.1
var. illyrica												
242 YUG	53	29	248	69	18	61	.66	.019	.87	8.8	.93	3.3
var. rhodopaea												
243 GRE	50	32	270	69	18	50	.57	.017	1.01	8.5	.86	2.7
551 GRE	51	30	259	62	20	52	.67	.018	.88	8.5	.90	2.6
var. armena												
221 TUR	54	36	306	74	32	85	.92	.016	.62	8.5	1.14	2.6
263 GEO	54	34	278	68	27	72	.77	.017	.69	8.1	.89	2.7
264 GEO	53	30	284	84	25	79	.81	.018	.81	9.5	1.05	3.3
261 GEO	52	30	255	70	29	63	.95	.017	.77	8.5	1.28	2.2
var. aquitana												
235 FRA	46	28	202	38	14	45	.50	.020	.65	7.2	1.20	3.5
239 FRA	46	28	249	59	18	60	.63	.017	.77	8.8	1.28	3.4
316 FRA	46	31	269	51	19	70	.63	.016	.58	8.7	1.19	3.6
320 FRA	48	27	228	49	19	44	.69	.019	.78	8.4	.91	2.4
238 FRA	44	28	238	56	18	50	.68	.017	.77	8.9	1.01	2.7
240 FRA	46	34	262	49	24	66	.71	.016	.56	7.8	.93	2.7
var. iberica												
245 SPA	54	46	312	81	51	76	1.13	.015	.64	6.9	.61	1.5
218 SPA	58	46	245	92	49	68	1.05	.020	.79	5.2	.51	1.4
LSD.10	2.8	3.0	41	8	2.7	10	.08	.002	.04	1.6	.17	.7
LSD.05	3.3	3.6	48	10	3.3	12	.09	.003	.04	2.0	.21	.8
LSD.01	4.3	4.8	64	13	4.3	16	.11	.004	.06	2.6	.28	1.1

Table 5. Growth data for Scotch pine provenances grown in the greenhouse for four and eight months, summarized by variety.

Variety	Length of Shoot	Length of Tap Root	Length of Lat. Root	Shoot	Tap Root	Lat. Root	Tap Root Wt./Unit Length	Top-Root Ratios: Top Length / Tot. Rt. Length	Top-Root Ratios: Top Weight / Tot. Rt. Weight	Root Ratios: Length: Total Lateral / Taproot	Root Ratios: Length: Longest Lateral / Taproot	Root Ratios: Weight: Lateral Root / Taproot
	mm.	cm.	cm.	---milligrams---			mg./cm.	-----number-----		---------number---------		
After Four Months Growth												
mongolica	37	17	96	32	9	20	.50	.032	1.09	5.6	.95	2.3
lapponica	37	19	105	23	7	20	.38	.030	.83	5.6	.77	2.8
septentrionalis	41	22	116	29	10	26	.48	.030	.90	5.7	.75	2.4
rigensis	43	22	130	33	10	26	.45	.028	.88	5.8	.86	2.7
altaica	43	24	154	38	10	36	.42	.024	.82	6.5	.83	3.7
polonica	48	24	187	55	14	40	.57	.023	1.02	7.6	1.00	2.9
hercynica	46	25	151	43	12	30	.48	.027	1.02	6.1	.72	2.6
haguenensis	52	27	212	58	14	42	.53	.022	1.07	8.0	.85	2.9
illyrica	49	23	187	59	18	51	.79	.024	.86	8.2	.95	2.8
rhodopaea	50	26	182	62	16	38	.60	.024	1.20	6.9	.98	2.4
armena	48	27	168	68	22	45	.79	.026	1.03	6.2	.76	2.1
aquitana	43	24	147	49	16	33	.69	.026	1.00	6.1	.85	2.1
iberica	51	39	171	85	43	46	1.21	.024	.91	4.4	.32	1.0
After Eight Months Growth												
mongolica	36	15	105	33	10	25	.47	.024	.94	5.4	1.01	2.8
lapponica	39	20	132	26	9	30	.42	.026	.68	6.5	1.01	3.6
septentrionalis	42	24	170	34	12	37	.49	.023	.71	7.0	.99	3.2
rigensis	43	26	181	36	12	44	.46	.021	.65	7.1	.93	3.7
altaica	43	26	198	42	11	46	.41	.020	.76	7.7	.97	4.5
polonica	50	27	268	58	14	61	.53	.018	.78	9.8	1.08	4.2
hercynica	49	27	226	48	14	50	.50	.020	.78	8.4	.98	3.7
haguenensis	55	29	331	60	15	65	.53	.016	.74	11.0	1.09	4.4
illyrica	53	29	248	69	18	61	.66	.019	.87	8.8	.93	3.3
rhodopaea	51	31	265	65	19	51	.62	.017	.95	8.5	.88	2.7
armena	53	33	281	74	28	75	.86	.017	.72	8.7	1.09	2.7
aquitana	46	29	241	50	19	56	.64	.017	.69	8.2	1.09	3.0
iberica	56	46	278	86	50	72	1.09	.017	.72	6.0	.56	1.4

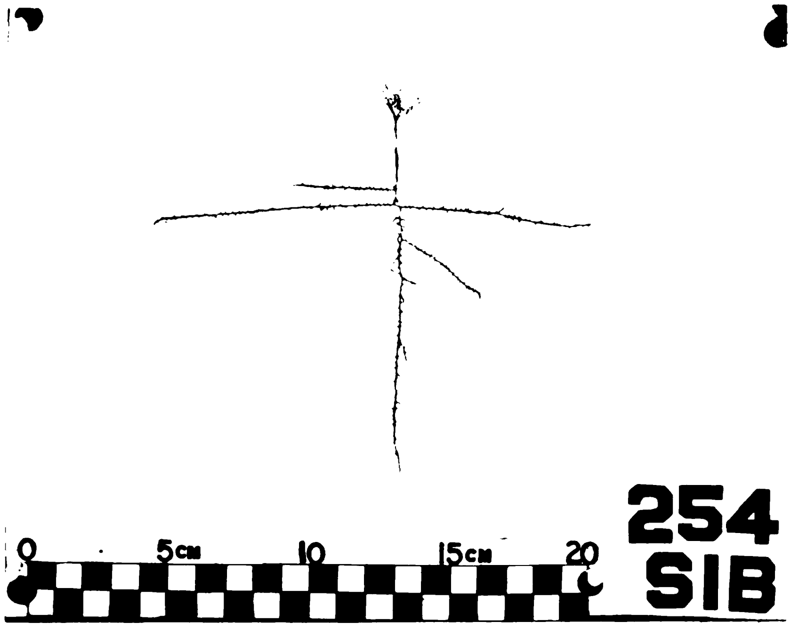
characteristic was expressed, particularly in relation to the type and extent of lateral root development, varied greatly between individual sources and between different varieties.

The Northern Varieties

These varieties cover the more northerly and colder portions of the Scotch pine range and include the following, as designated by Ruby (1964): mongolica from northern Siberia; lapponica from north-central Scandinavia; septentrionalis from southern Norway, south-central Sweden, southern Finland and adjacent parts of the USSR; rigensis from southern Sweden, Lativia, and adjacent parts of the USSR; and altaica from southern Siberia. All northern varieties were characterized by distinct tap root development, with lateral root extension generally restricted to branching from the upper portions of the tap root. There was very limited lateral extension from the lower portions of the tap root (Figures 2, 4, 5, 6, and 7).

One source of var. mongolica, MSFG 254 from northeastern Siberia, was distinct in a number of ways (Figure 2). It was the smallest of all seed sources in all aspects of top and root development. Depth of tap root was limited, more so than lateral root extension, so that the length ratio of longest lateral to tap root was high for this source (Tables 3, 4, 5). The area from which seed of MSFG 254 was collected has a very severe climate (Table 1). The average annual temperature is extremely low (-11.6° C), the growing-season temperature is relatively warm (8.1° C), and rainfall is extremely low (145 millimeters). It appears that root systems of this source are adapted to this combination of factors. Shallow depth of rooting is probably an adaptive character correlated with permafrost at a shallow depth in the soils of the region. The growing season aridity index for the area from which MSFG 254 was collected is low and the large lateral

Figure 2. Seedling of MSFG 254, a seed source of var. mongolica in northeastern Siberia, after four months growth.



root extension in relation to tap root length may be a response to the dry growing season.

Root characteristics of the Scandinavian varieties generally varied on a north-south gradient. However, MSFG 546 and 273 had much less lateral root growth than did many sources from further north. Root development (in terms of both depth of rooting and lateral extension) and top growth were better correlated with annual temperature than with latitude of origin (Figure 3). First year height growth data for seedlings of the same sources grown in the nursery (from Wright and Bull's data) also showed correlation at the one percent level with average annual temperatures ($r = 0.86$).

Lateral root development of seedlings of north-Swedish MSFG 549 was similar to that of Siberian 254. However, tap roots were much longer in 549 than 254, possibly because average annual temperature was much higher (0.6° C) in northern Sweden than in northeastern Siberia (-11.6° C). Permafrost, if present, was probably deeper in the soils of the area from which MSFG 549 was collected. This same characteristic of relatively greater tap root lengths in relation to lateral extension which was shown by MSFG 549 was common to all of the Scandinavian sources. Maximum tap and lateral root growth of the Scandinavian sources was shown by MSFG 550, the provenance from the most southern -- and warmest -- area from which seed was collected. Root development of three Swedish sources (MSFG 549, 541 and 550) is illustrated in Figures 4, 5, and 6.

Attempts to correlate root development of Scandinavian sources with annual or growing season precipitation failed, possibly because moisture is not a critical factor in Scandinavia. (Notice the

Figure 3. Relationship between eight month growth of seedlings of Scandinavian origin and average annual temperature of the area from which seed was collected.

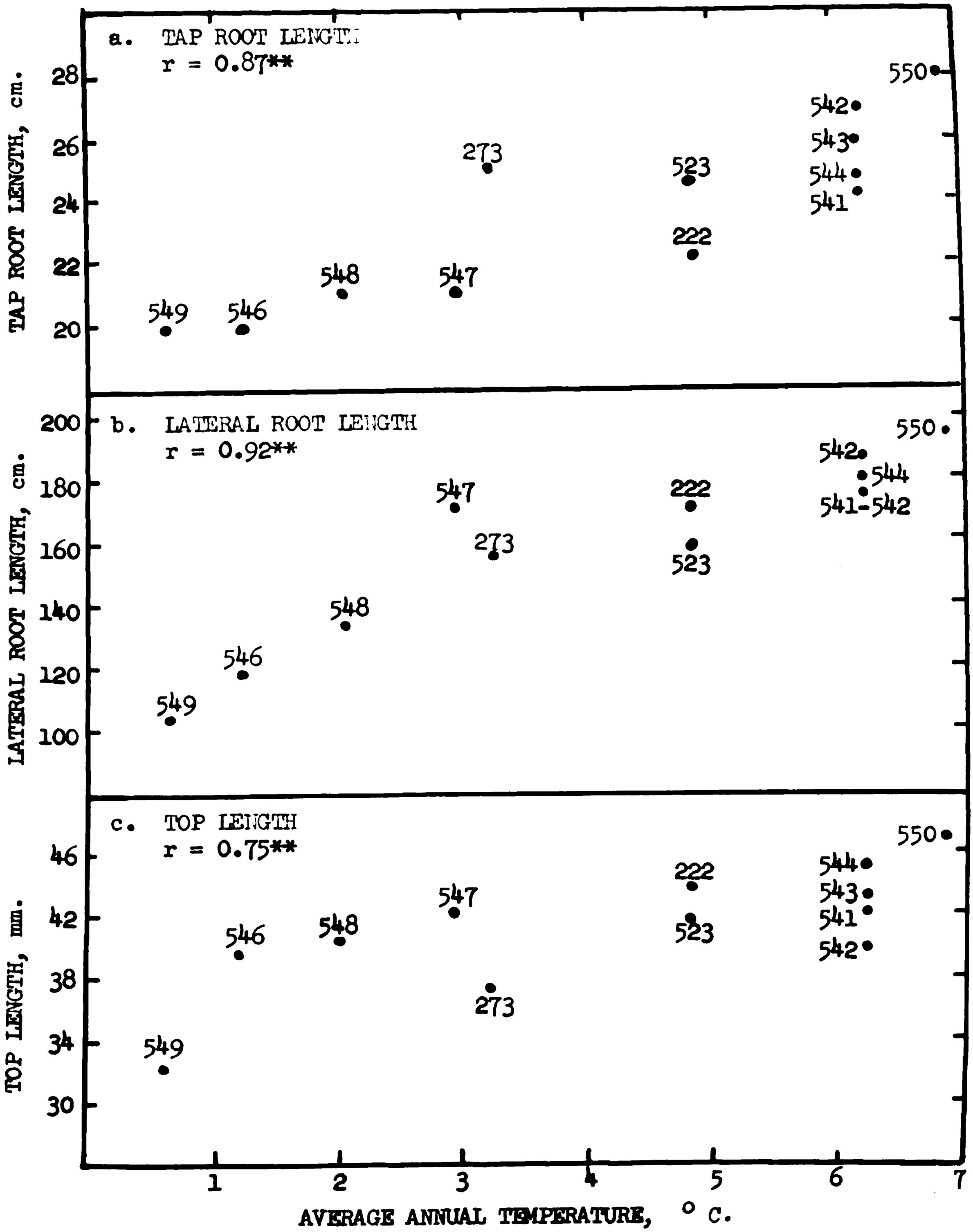

a. TAP ROOT LENGTH
r = 0.87**
TAP ROOT LENGTH, cm.
b. LATERAL ROOT LENGTH
r = 0.92**
LATERAL ROOT LENGTH, cm.
c. TOP LENGTH
r = 0.75**
TOP LENGTH, mm.
AVERAGE ANNUAL TEMPERATURE, ° C.
549
546
548
547
273
523
222
542
543
544
541
550
541-542

Figure 4. Seedling of MSFG 549, a seed source of var. lapponica in northern Sweden, after four months growth.

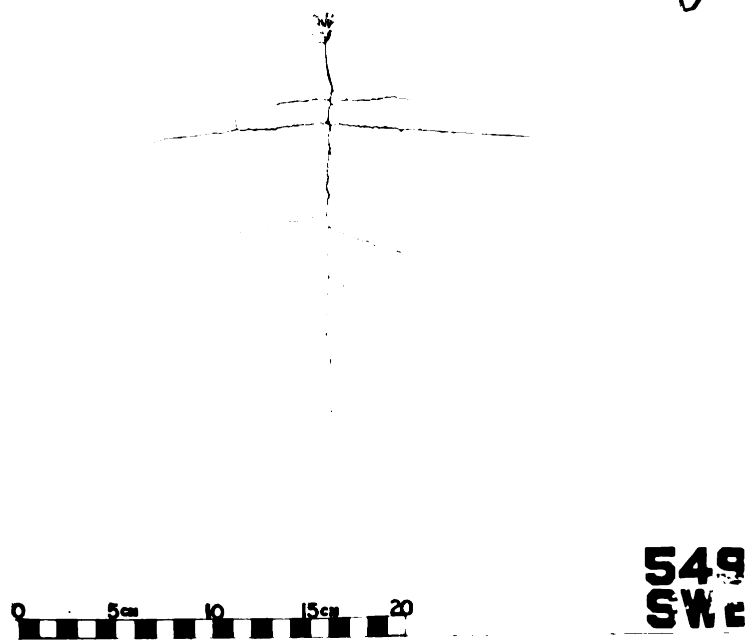


Figure 5. Seedling of MSFG 541, a seed source of var. rigensis in south-central Sweden, after four months growth.

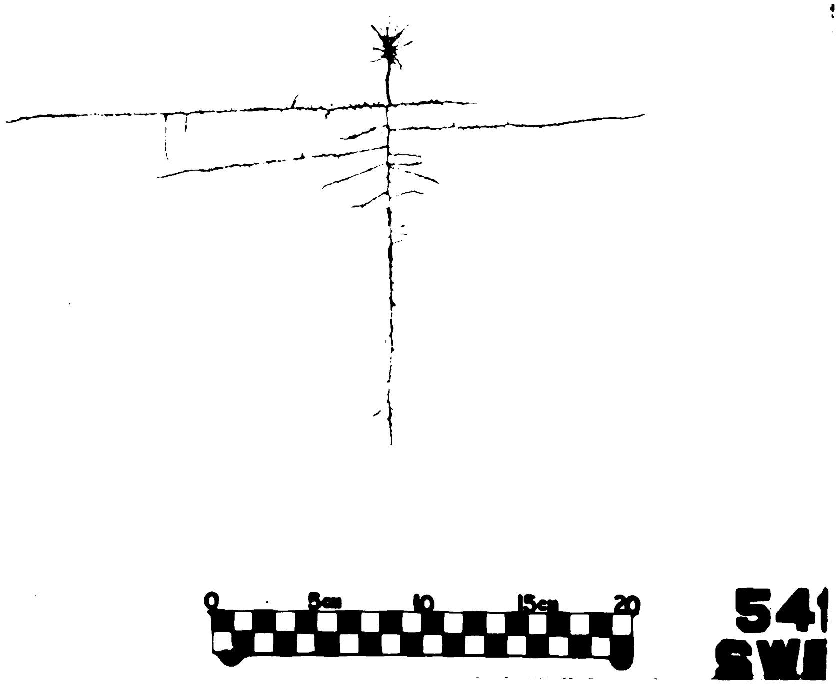
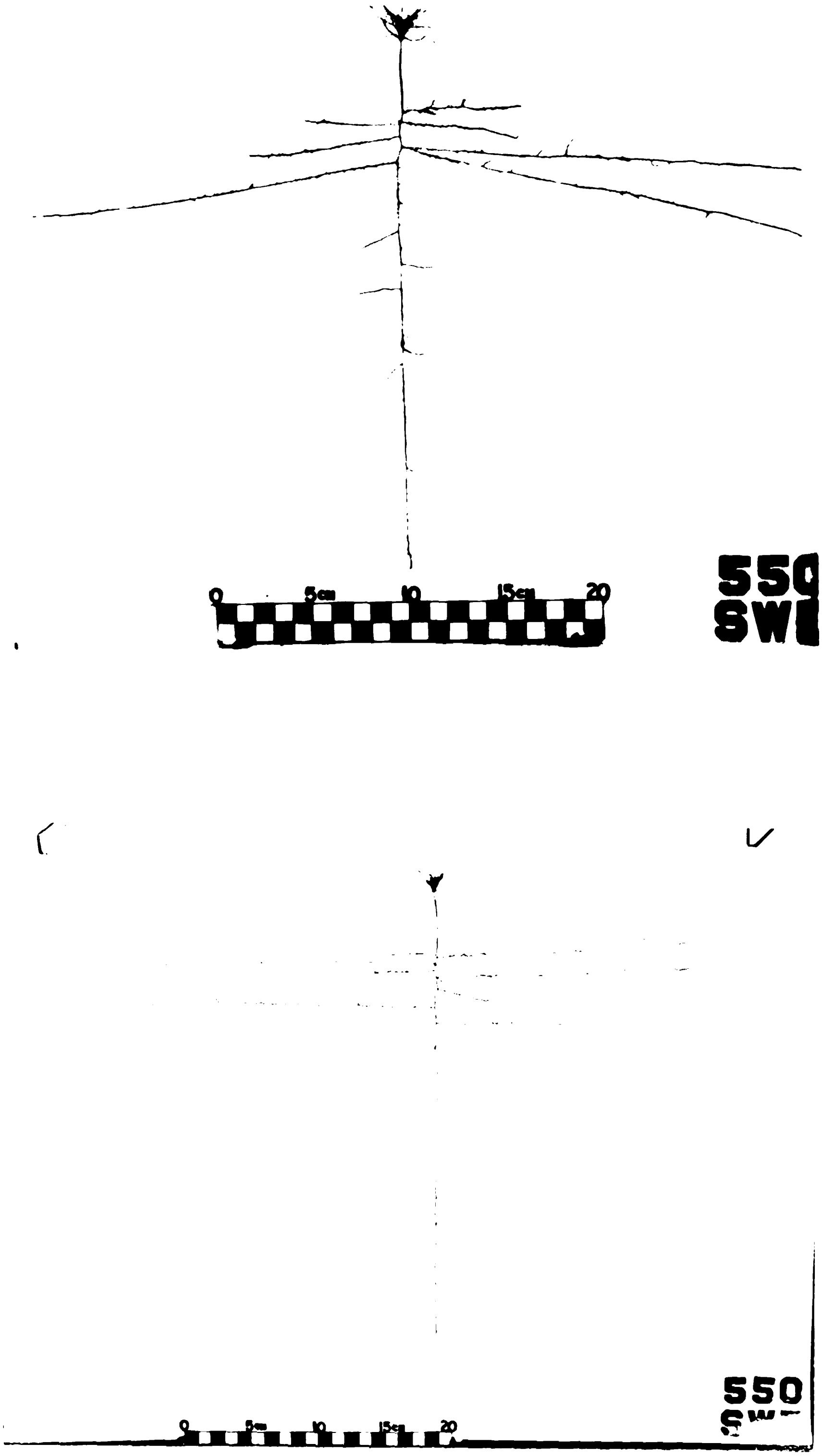


Figure 6. Seedlings of MSFG 550, a seed source of var. rigensis from the southern tip of Sweden, after four (top) and eight (bottom) months growth.

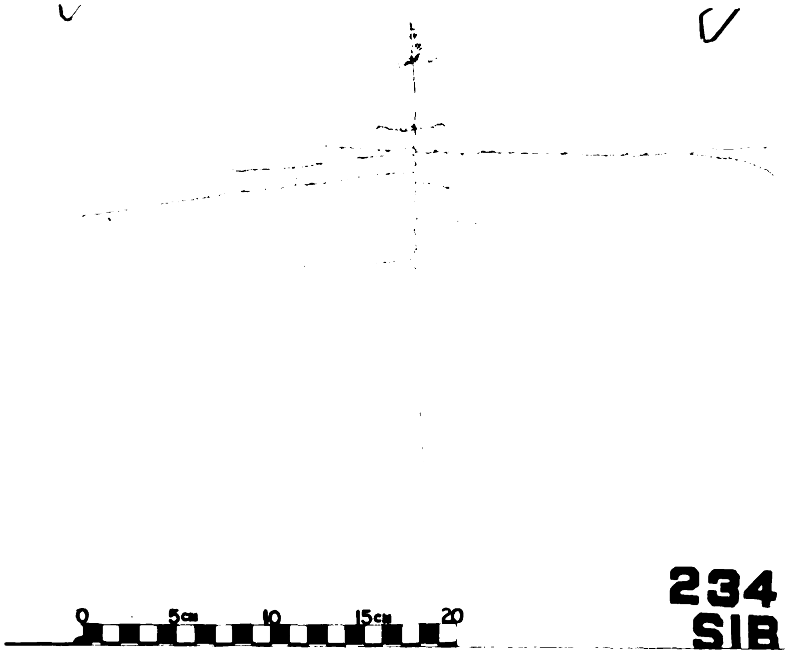


uniformly high aridity index values for Scandinavian provenances in Table 1).

Ruby recognized two varieties of Scotch pine in central and eastern Siberia -- var. mongolica (254, 255) in the north and east and var. altaica (234, 256) in the Altai Mountain region of central Siberia. In doing this he used previous varietal descriptions published by the Russians, while recognizing the possibility that recognition of more taxonomic entities might be warranted. In my work, the two seedlots of var. altaica were similar to each other and similar to seedlings of var. rigensis from southern Sweden, despite the fact that the Siberian climate is much more rigorous than that of southern Sweden (Table 1).

The two seedlots of var. mongolica differed markedly, as they did in Wright and Bull's (1963) earlier study. MSFG 254, from the far north, had very slow top growth, a short tap root, and a high ratio of lateral to tap root length. MSFG 255, from southeastern Siberia, had faster top growth and a moderate ratio of lateral to tap root length. Root characteristics of MSFG 255 were very similar to those of the central Scandinavian var. septentrionalis.

Figure 7. Seedling of MSFG 234, a seed source of var. <u>altaica</u> in central Siberia, after four months growth.



The Central European Varieties

Origins from the following varieties from the central European area were used in the study: polonica from northeastern Poland; hercynica from Germany and Czechoslovakia; haguenensis from Belgium, northeastern France (Vosges Mountains), and western West Germany; and illyrica from Yugoslavia. Root characteristics of seedlings from central Europe were distinctly different from those of Scandinavian sources. Central European sources had more moderate expression of the tap root characteristic and more extensive lateral root extension along the major portion of the tap root than did origins from further north (Figures 8, 9, 10).

Varieties haguenensis and polonica were similar in root characteristics, but were different from other central European types. Seedlings from these varieties had much longer lateral roots than did provenances from almost any other portion of the species range. Belgian seedlings (MSFG 530) of var. haguenensis had the greatest lateral length of all. Because of the extensive lateral lengths, origins from these varieties had the most favorable balance between top length and lateral root length. In some cases side extension of lateral roots was very great in relation to depth of rooting (Figure 8). In other cases, lateral roots were concentrated in a columnar area close to the main tap root (Figure 9).

The origins from varieties polonica and haguenensis were also more branched than those from other portions of the species range (Table 6).

Wright and Bull (1963), Wright and Baldwin (1957), and Wright

Table 6. Number of lateral roots per tree and proportion of lateral roots having no, one, two, three or four branches of Scotch pine at ages four and eight months.

Variety	Total Lateral roots per tree at ages		Proportion of total laterals								
			at 4 months				at 8 months				
			Number of branches				Number of branches				
	4 months	8 months	0	1	2	3	0	1	2	3	4
	----number----		---------------percent of total---------------								
mongolica	453	606	96.4	2.8	.8	.0	96.6	2.0	1.4	.0	.0
lapponica	429	540	96.5	2.3	1.2	.0	96.3	2.2	1.5	.0	.0
septentrionalis	516	694	95.6	2.8	1.6	.0	96.3	2.2	1.5	.0	.0
rigensis	566	670	96.5	2.3	1.2	.0	95.7	2.5	1.8	.0	.0
altaica	725	705	96.7	2.3	1.0	.0	96.3	2.1	1.6	.0	.0
polonica	806	1097	96.7	2.1	1.2	.0	95.8	2.0	2.0	.0	.0
hercynica	654	783	96.0	2.5	1.5	.0	95.5	2.5	2.0	.0	.0
haguenensis	884	1198	95.9	2.2	1.8	.1	96.0	1.8	2.1	.1	Trace
illyrica	772	932	96.6	2.3	1.1	.0	96.8	2.1	1.0	.1	.0
rhodopaea	760	939	96.9	2.2	.9	.0	96.1	2.1	1.8	Trace	.0
armena	703	1193	96.3	2.6	1.1	.0	96.9	1.8	1.3	Trace	.0
aquitana	581	933	96.2	2.8	1.0	.0	97.1	1.9	1.0	Trace	.0
iberica	680	1193	95.6	3.5	.9	.0	96.9	2.3	.8	.0	.0

Figure 8. **Seedlings of MSFG** 530, **a seed source of var.** __**haguenensis**__ **in Belgium, after four (top) and eight (bottom) months growth.**

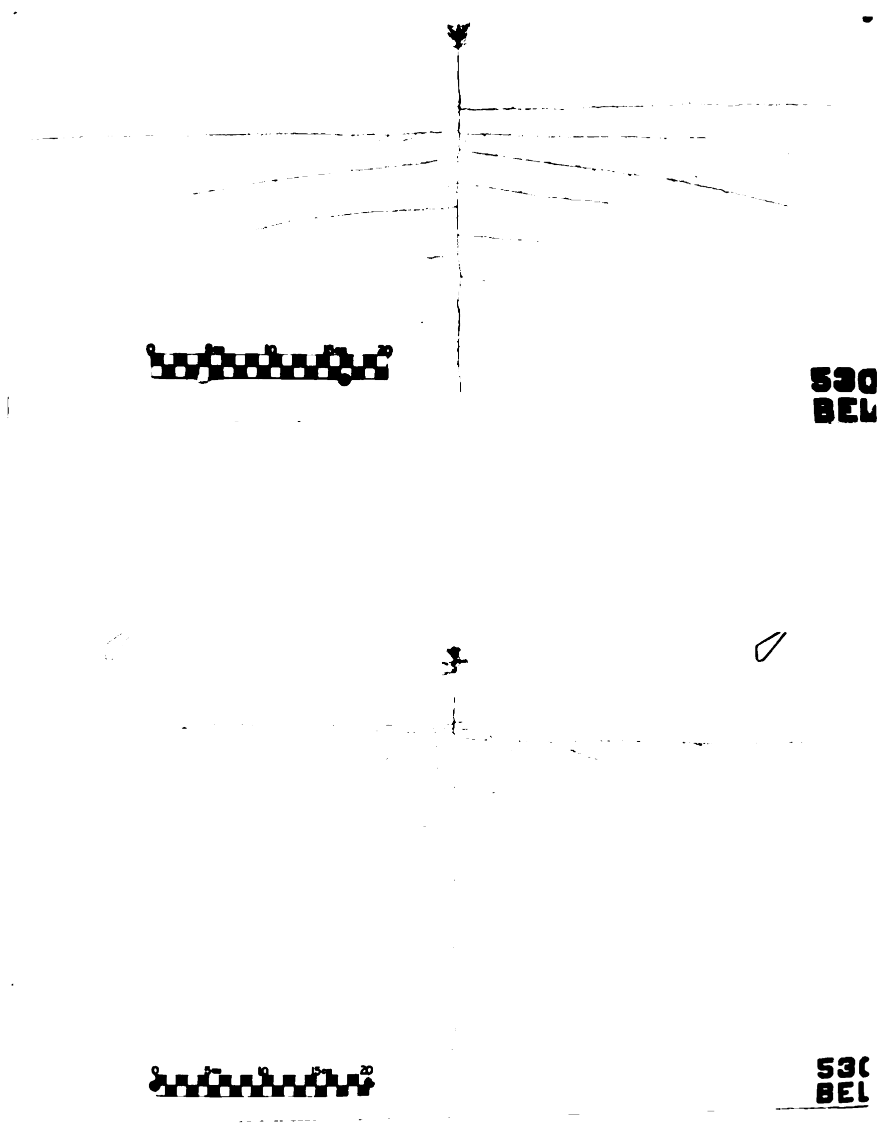
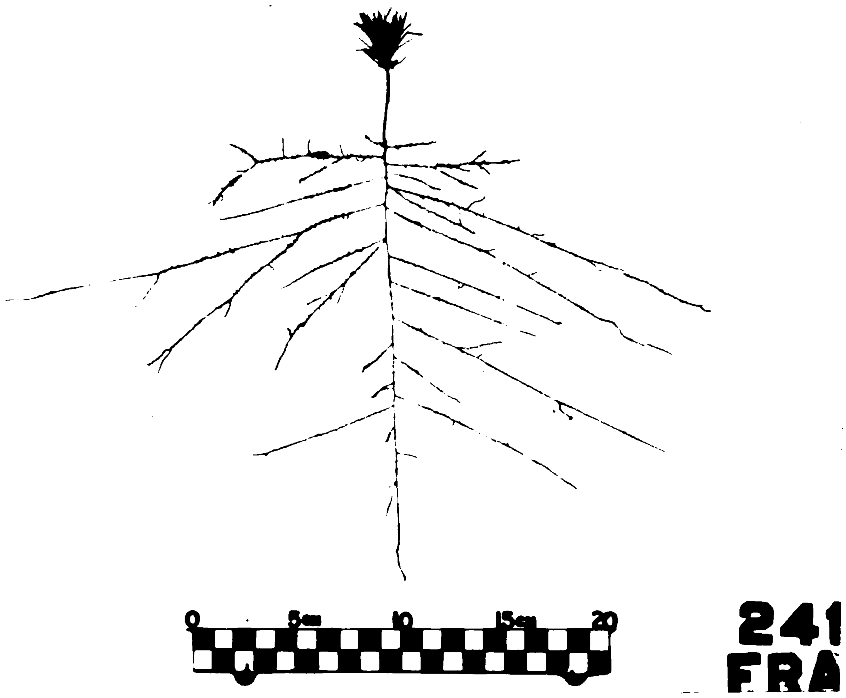


Figure 9. Seedlings of MSFG 241, a seed source of var. haguenensis in northeastern France, after four (top) and eight (bottom) months growth.



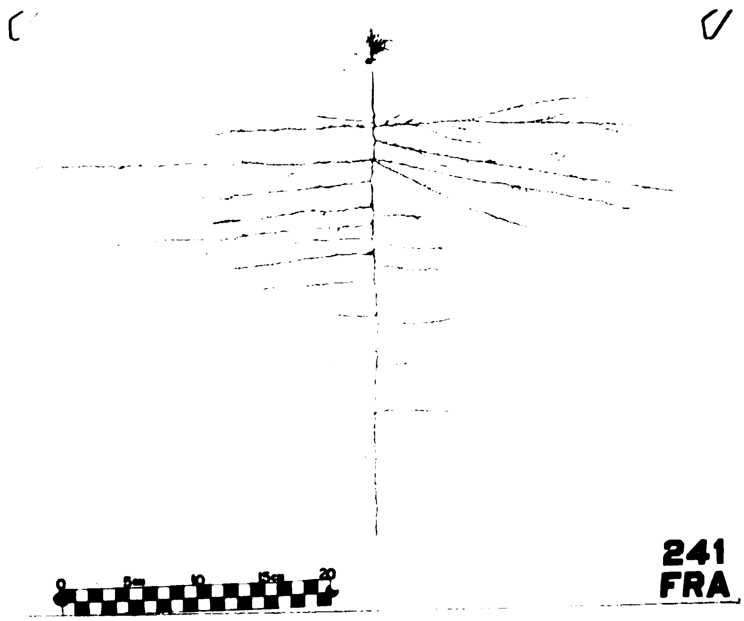
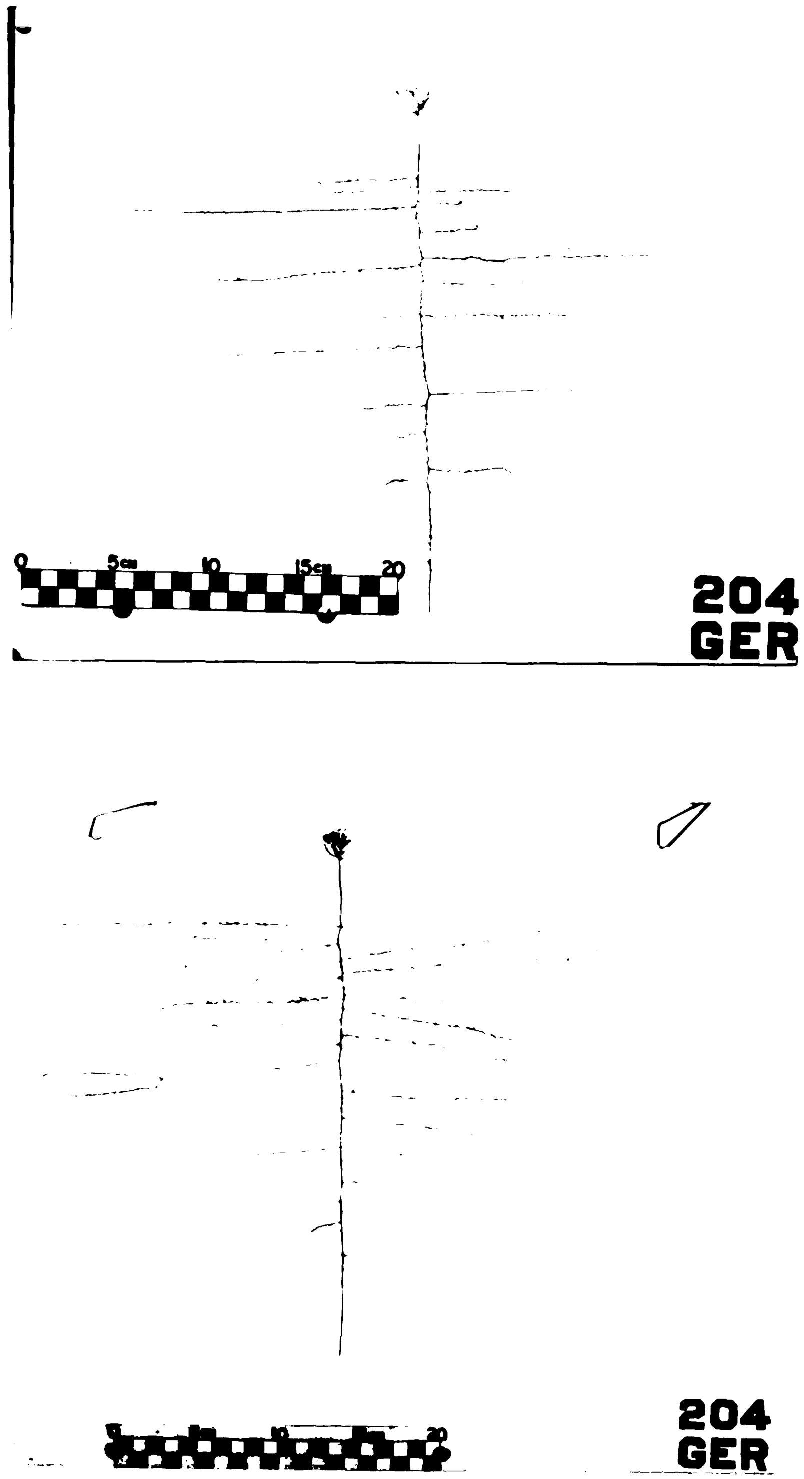


Figure 10. Seedlings of MSFG 204, a seed source of var. hercynica from Germany, after four (top) and eight (bottom) months growth.



et al. (1966) found that the fastest growing provenances of Scotch pine came from varieties polonica and haguenensis. It seems probable that the rapid growth of these varieties is associated with the extensive lateral lengths and branching of the root systems. Roots of these seedlings occupy very completely the volume of soil in which they are growing, making maximum use of soil moisture and nutrients in the rooting zone.

The sources from variety herecynica were similar to those of var. haguenensis except that they had consistently smaller lateral root lengths and they were less branched (Figure 10). MSFG 242 from Yugoslavia (var. illyrica) had root characteristics unlike those of other central European provenances to which it is similar in foliage and growth. This source, from an isolated portion of the range to the south of the continuous range common to the central European types, had roots similar to some of the southern varieties.

Unlike the Scandinavian sources, root characteristics of central European sources, were not correlated closely with climate at place of origin. This is possibly the result of free interchange of genes in the more or less continuous population and climatic fluctuations in post-Pleistocene time. There is usually a lag between climatic change and evolutionary response to that change so that one need not expect perfect adaptation of modern genotypes to their particular microenvironments.

The Southern Varieties

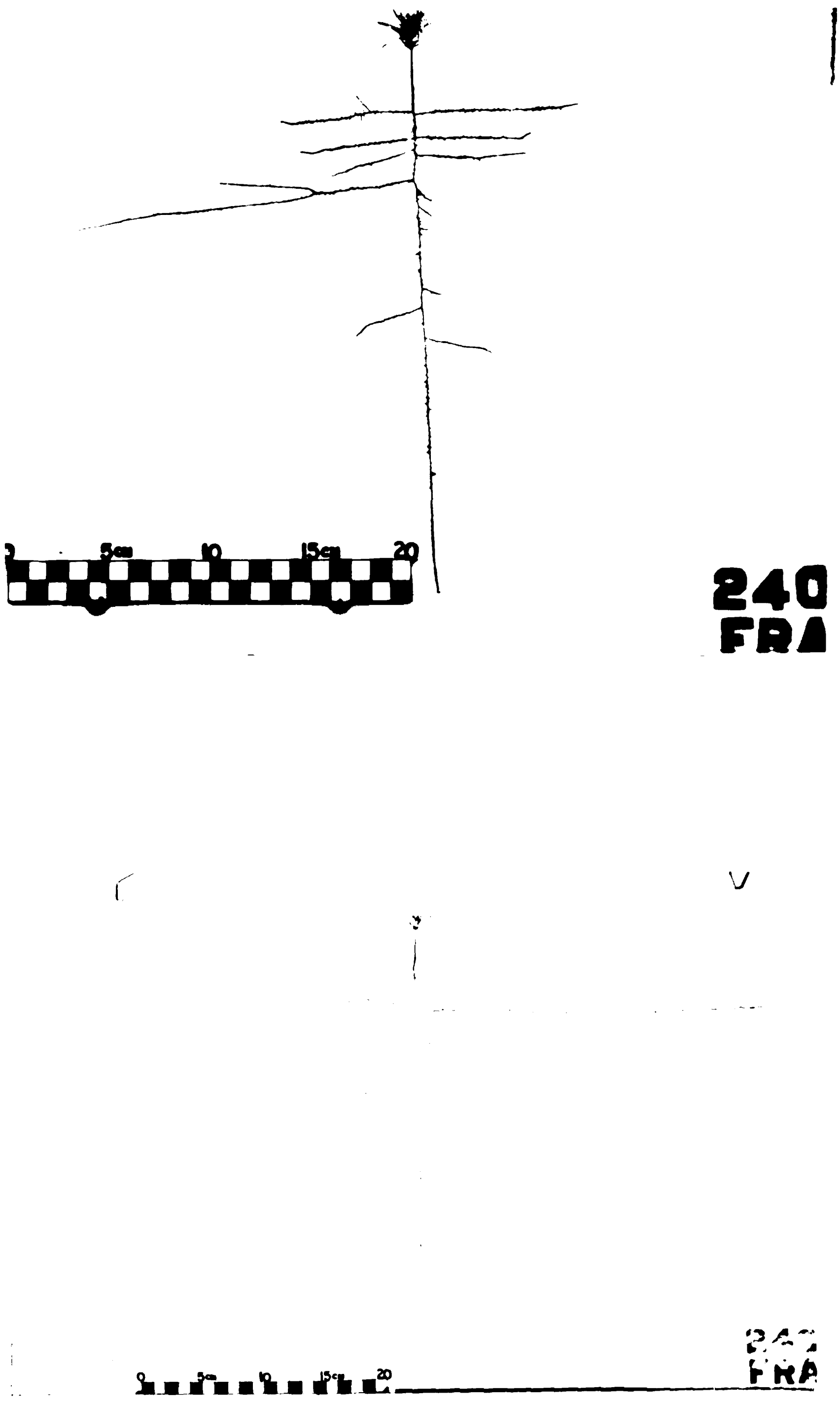
These varieties cover the discontinuous southerly portions of the Scotch pine range and include the following varieties: var. aquitana from the Central Massif of France; var. iberica from Spain; var. rhodopaea from Greece; and var. armena from Turkey and the Georgian SSR. As a group these varieties differed from those of northern and central Europe. In many characteristics the southern varieties also varied from each other.

All southern origins were tap rooted. This was expressed in general appearance and high weight per unit length of the roots. They also had less branching of the lateral root systems (Table 6). Tops of southern seedlings were heavier per unit length than those from northern and central European varieties (Tables 3, 4, 5).

Seedlings from the Central Massif of France (var. aquitana) had root systems similar in appearance to those of northern varieties. They were tap-rooted and the majority of lateral roots grew from the upper portions of the tap root (Figure 11). Lateral root lengths for this variety were generally longer than those of the northern varieties and were comparable to those of central European var. hercynica. Root systems of var. aquitana were less branched than in var. hercynica however (Table 6). Top weight per unit length was also higher for var. aquitana than for central European or northern origins.

Root length was not correlated with climate at place of origin within var. aquitana. Neither could the similarities in root types between these sources and northern ones be explained on the basis

Figure 11. Seedlings of MSFG 240, a seed source of var. aquitana in southern France, after four (top) and eight (bottom) months growth.

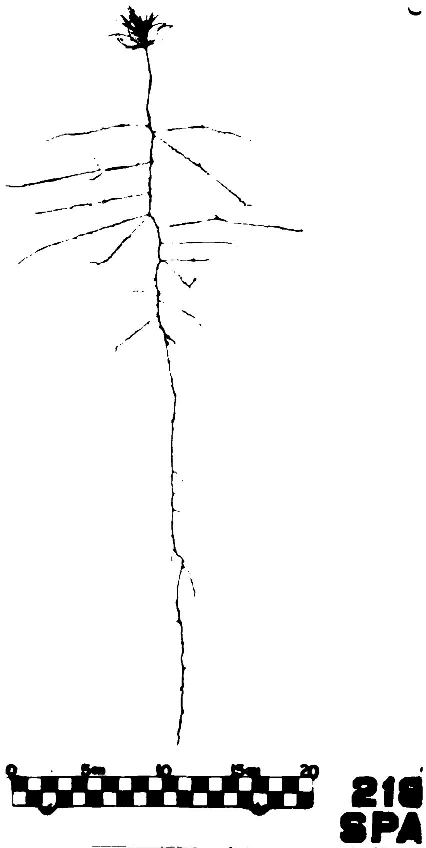


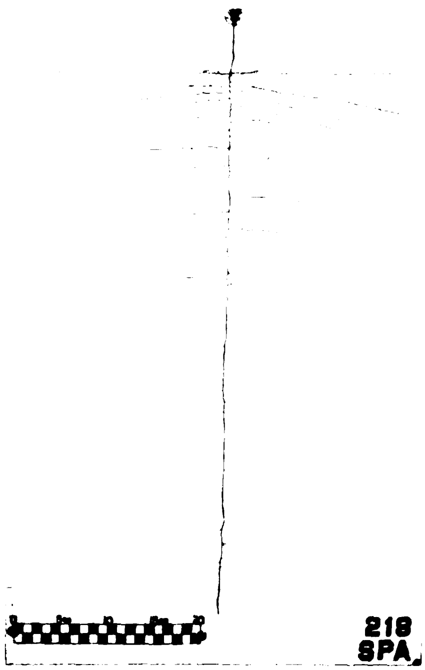
of climate. Temperatures in the central Massif are generally much higher than in northern Sweden and Siberia. It is possible that this root type may reflect an evolutionary response to weather conditions during Pleistocene glaciation. At that time, prevailing temperatures in the Central Massif would have been much colder than at present. This might have favored the development of types having lateral rooting near the surface areas, just as in present northern varieties.

The two sources from Spain (var. iberica) had the most distinctive root systems of all sources investigated (Figure 12). They had significantly longer tap roots than all other origins. Weight per unit length of the tap root was also significantly greater than in any other source, northern or southern. Lateral roots were generally short, but numerous and extended from along most of the tap root length. As a result the root systems had a narrow, columnar appearance, with the highest percentage of total root weight in the tap-root. Lateral roots of var. iberica had the fewest branches per unit of length of all sources.

The tops of Spanish seedlings were also significantly heavier in relation to their length than in other origins. This was not due to greater number or weight of needles, but to diameter (and possibly density) of the stem. The strong tap roots of Spanish origins appear to be adaptive to Spanish climatic conditions (Table 1). Temperatures there are relatively high and precipitation is low. Effective precipitation is very low, as indicated by the small aridity index values. There are periods during mid-summer when precipitation

Figure 12. Seedlings of MSFG 218, a seed source of var. *iberica* in Spain, after four (top) and eight (bottom) months growth.





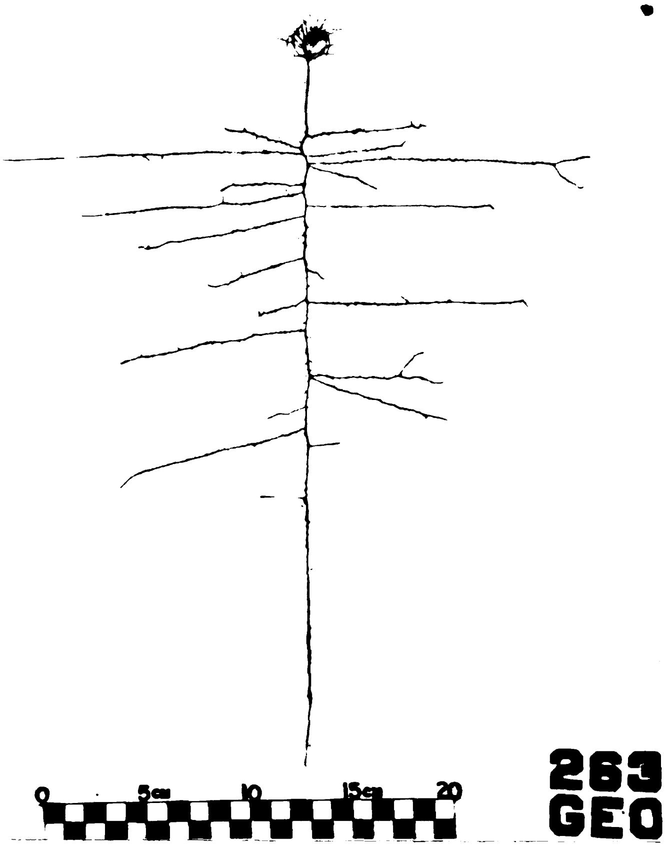
is only 10 to 20 millimeters per month. Under these conditions seedlings having a deep tap root with laterals concentrated along its length have a decided advantage in withstanding soil moisture depletion and drought conditions in the surface layers.

The seedlings of var. armena and var. rhodopaea came from three isolated areas in southern portions of the Scotch pine range -- from Greece, Turkey and the Gerogian SSR (Figure 1). All of these sources exhibited less branching than sources from further north, but none had the narrow, columnar root type of var. iberica nor lateral rooting confined to the upper portion of the tap root as in var aquitana (Central Massif of France).

Greek origins (var. rhodopaea) were characterized by less pronounced tap root development than those from Georgia and Turkey (var. armena). The Greek provenances exhibited lower weights per unit length and more branching of lateral roots than did seedlings of var. armena. The Turkish and Georgian sources (Figure 13) were nearly alike except that the Turkish origin had deeper tap roots.

Differences between var. armena and var. rhodopaea are probably associated with climatic differences. The Greek provenances were collected from areas with very high rainfall and comparatively low temperatures, resulting in very high aridity index values. The Turkish and Georgian seed, on the other hand, were collected in areas of limited precipitation and comparatively high temperatures, resulting in very low effective precipitation. The lower weight per unit length of tops and root systems of the Greek sources was apparently a reflection of the more moist conditions under which they grow naturally. In this respect the Greek and south French sources

Figure 13. Seedling of MSFG 263, a seed source of var. armena in the Georgian SSR, after four months growth.



are similar.

The distinct differences between the Georgian-Turkish and Greek populations may be explained by the migration barrier between the two, and the relatively slight differences between Turkish and Georgian sources to the absence of a distinct migration barrier.

Evolutionary Development of Root Systems

The root characteristics of different geographic origins of Scotch pine are as distinct in many ways as the top characteristics described by Wright and Bull and Ruby for the same seed origins. In most cases the variation in root type coincided with the variation in top characteristics. In a few, however, variations in root type should be used as the basis for modification of the described varieties.

Evolution of root systems appears to reflect the degree of isolation, Pleistocene history, and prevailing climatic conditions in the area of seed collection. In southern areas the trees grow in more or less isolated stands located at high elevations. These forests were south of the polar ice cap during Pleistocene times. Evolution has probably proceeded uninterrupted for a much longer time than in central or northern Europe where the species was obliterated during glaciation except for remnants in some of the higher mountainous areas. Exchange of genetic material between the Central Massif of France, Spain, Greece, Turkey, the Georgian SSR, and possibly Yugoslavia was limited. The distinct root types are apparently a reflection of this isolation. Turkish, Georgian and Spanish origins show adaptation to the warm, dry climate which prevails while Greek origins reflect the more moist climate of the area from which seed was collected. In the Central Massif of France, isolation has apparently contributed to a distinct genetic lag between root types and prevailing weather conditions. Seedlings from this area have root systems which appear to have developed in response to Pleistocene climatic conditions.

During Pleistocene glaciation, most of the range of Scotch pine in northern Europe and Asia was obliterated. The surviving remnants, probably in the Scandinavian highlands, the Ural Mountains or a part of Siberia, were well differentiated prior to glaciation. Reintroduction of the species occurred from these well-differentiated remnants and extensive and more or less continuously forested areas were eventually formed. Exchange of genetic material has probably been quite free over large regions. Root types within regions apparently developed in response to selection pressures operative in particular areas, although it is also probable that sources still reflect their pre-Pleistocene ancestry to a considerable extent. Temperature variations appear to have been the principal factors affecting differentiation in the northern areas.

The central European region had a different evolutionary history. Most of the region was covered by Pleistocene glaciation. Repopulation probably occurred from the north and south -- from the Scandinavian highlands and possibly the Urals in the north and from the Alps and Carpathian Mountains in the south. This reinvasion from well differentiated pre-Pleistocene remnants eventually formed extensive and nearly continuous stands. This provided for a free interchange of genes in most areas. Because of the diversity of pre-Pleistocene remnants, the genetic base from which the modern central European populations evolved was probably much greater than in the northern or southern portions of the Scotch pine range. Root types of provenances from the central European area appear to reflect this free interchange of genetic material and diverse gene pool.

CHAPTER IV

EARLY ROOT DEVELOPMENT PATTERNS
OF SCOTCH PINE PROVENANCES

A number of investigators have studied the seasonal patterns of root growth of different tree species. As reviewed by Kramer (1949) and Kramer and Kozlowski (1960), these studies have generally demonstrated large differences between species in such factors as rate of growth, total amount of growth, length of the growing season, cyclic nature of growth periods and optimum growth requirements.

There has been little work, however, relating differences in root development for provenances of the same species. Leibundgut and Dafis (1962 and 1964) found variations in rates, duration and total amount of root growth of different central European origins of Scotch pine and European larch. They noted differences in time of completion of the grand period of root growth, but not in the time when growth started.

Differences in root elongation might also be implied from differences in top growth patterns. Wright and Bull (1963) reported variation of over two months in date of first-year bud set between the most northerly and southerly provenances of Scotch pine used in their study. Brown (1967) found differences in seasonal rate of top growth and length of the growth period for five provenances of Scotch pine from western Europe.

PROCEDURE

Eight seed sources of Scotch pine were selected representing a north-south transect through western Europe, plus one source from the southeastern part of the range and one from central Siberia (Table 7). Each seedlot was originally gathered by cooperators in Europe and Asia for use in the Scotch pine provenance study conducted by Wright and Bull (1963). Seed collections were made from ten or more average trees, usually in stands of several acres in size. The climatic data were compiled by John L. Ruby (1964) and are from weather stations located as closely as possible to the stands from which the seeds were collected. In most cases the data apply to the area of collection; in some to stations some miles from locations of collection. An "Index of Aridity" was calculated using DeMartonne's (1926) formula: Index = $\frac{\text{precipitation in mm.}}{\text{temp. in } ^{\circ}\text{C.} + 10}$. The smaller the index value, the drier the climate.

Seed was sown in individual containers in the greenhouse in January 1965, with five seed per container. The containers were approximately 8 inches deep and 4 inches square. Five replicates, with two tree plots, were used and the two trees in each plot were located in adjacent containers on the greenhouse benches. Germination began nine days after sowing. Five days later the seedlings were thinned to one per container. The seedlings were two days old and still retained their seed coats.

The potting mixture used consisted of one-third (by volume) each of builders sand, peat moss, and a sandy loam nursery soil. A complete fertilizer was added to this mixture to provide approximately 50 ppm each of N, P_2O_5, and K_2O. This medium provided conditions for

Table 7. Location and climate at place of origin of Scotch pine seed seed sources used in study of root development patterns.

MSFG No. (a)	Country of Origin	Lat. N.	Long. E.	Elev.	Temperature		Months Above		Precipitation		Index of Aridity (b)	
					Annual	April-Sept.	0°C.	6°C.	Annual	April-Sept.	Annual	April-Sept.
		°	°	feet	°C.	°C.	---number---		--millimeters--		------number------	
547	Sweden	62.5	15.7	700	2.9	9.1	7	5	525	332	40.7	17.4
543	Sweden	59.9	12.0	700	6.2	12.6	8	6	630	347	38.9	15.4
256	Siberia	56.7	96.3	1300	1.8	9.3	5	5	241	191	21.1	9.9
307	Czech.	49.9	17.9	800	8.8	15.5	9	7	630	407	33.5	16.0
253	Germany	49.1	7.8	1300	9.5	15.0	12	7	612	338	31.4	13.5
239	France	45.3	3.7	3100	9.0	13.9	12	7	780	503	41.1	21.0
243	Greece	41.5	24.2	5600	7.4	12.7	10	7	2460	1190	141.4	52.4
245	Spain	40.7	-4.2	4900	11.9	17.5	12	9	508	264	23.2	9.6

(a) Numbers are those used in the Michigan State Forest Genetics accession record.

(b) Index of Aridity: (Demartonne, 1926) $\text{Index} = \dfrac{\text{Precipitation in mm.}}{\text{Temperature in °C.} + 10}$

unrestricted rooting and recovery of root systems with a minimum of damage. The seedlings were watered at intervals to keep moisture near field capacity.

Ten days after germination the first lot of containers was taken from the greenhouse and the root systems were carefully washed and measured. This procedure was repeated five more times at two week intervals, giving a sequence at ages 10, 24, 38, 52, 66, and 80 days after germination. Data for each individual sampling were analyzed separately by analysis of variance using means of the 2-tree plots as items (Table 8).

Table 3. Analyses of variance for root growth of Scotch pine progenies sampled at 14-day intervals (a).

Factor	F ratio at ages					
	10 days	24 days	38 days	52 days	76 days	80 days
Tap root length	3.4**	5.3***	14.1***	11.5***	8.7***	7.3***
Lateral root length	2.6*	2.2	5.4***	6.1***	6.8***	13.2***
Tap root weight	--	--	--	28.9***	19.9***	52.0***
Lateral root weight	--	--	--	11.7***	8.3***	8.8***
Total root weight	11.7***	14.2***	24.6***	22.3***	15.9***	21.9***
Tap root weight per unit length	--	--	--	12.8***	10.0***	17.0***
No.: Total Lateral Roots	2.3*	14.2***	2.8***	3.3*	8.8***	12.5***
No.: Lateral Roots, Unbranched	2.8*	2.1	2.7*	3.3*	8.5***	12.1***
No.: Lateral roots, 1 branch	--	--	2.9*	5.5***	5.3***	6.5***
No.: Lateral roots, 2 branches	--	--	--	--	3.5**	12.0***
Lateral Root Length / Tap Root Length	2.6*	4.5**	4.4**	4.3**	4.0**	6.9***

(a) With 7 degrees of freedom in treatment (seed source) mean square and 28 degrees of freedom for error mean square.

* Significant at 5 percent level.
** Significant at 1 percent level.
*** Significant at 0.1 percent level.

ROOT DEVELOPMENT PATTERNS

All sources exhibited distinct tap root development throughout the eighty-day sampling period. The lengths of the tap and lateral roots varied considerably among sources however.

Initial root development of all origins was confined exclusively to tap root extension (Table 9, Figures 15-22). At ten days a few sources showed traces of lateral root formation, but there were no appreciable number of laterals until 38 days after germination. In general, lateral root length did not exceed tap root length until 52 days after germination.

The rate of tap root elongation remained nearly constant for the first 24 to 38 days, depending on seed source. Then the rate generally declined. Lateral root elongation showed an opposite type of development. It was very slow during the time when tap root growth was greatest. After tap root elongation declined, lateral length increased rapidly in each successive 14-day period (Figure 14, Table 9).

Northern Provenances. The northern origins were MSFG 547 and 543 from Sweden and MSFG 256 from central Siberia. They had some characteristics in common to distinguish them from more southern origins. Early tap root elongation was more rapid than in more southern provenances. This was particularly so in Siberian 256. At each of the first five samplings, seedlings of this provenance attained the highest proportion of total tap root elongation of all sources. They completed over 90 percent of 80-day tap root extension by the 52nd day (Table 11).

Table 9. Root lengths of Scotch pine provenances measured at 14-day intervals.

Seedlot, Country of Origin(a)	Tap Root Length 10 days	24 days	38 days	52 days	66 days	80 days	Lateral Root Length 10 days	24 days	38 days	52 days	66 days	80 days	Ratio: Lateral Root Length / Tap Root Length 10 days	24 days	38 days	52 days	66 days	80 days
	millimeters						millimeters						ratio					
Northern Origins																		
547 SWE	40	85	129	155	174	178	1	27	110	203	290	483	.009	.31	.83	1.32	1.66	2.73
543 SWE	44	101	154	188	199	217	1	39	147	314	436	709	.032	.29	.96	1.68	2.19	3.30
256 SIB	51	104	163	206	222	221	2	42	215	352	552	819	.045	.39	1.34	1.70	2.50	3.73
Central European Origins																		
307 CZE	41	102	157	197	201	231	1	34	151	268	461	859	.033	.33	.96	1.36	2.31	3.73
253 GER	47	110	167	203	219	249	1	34	145	374	551	1138	.030	.30	.85	1.85	2.56	4.62
Southern Origins																		
239 FRA	45	105	166	210	222	258	1	21	123	225	343	651	.012	.20	.74	1.10	1.55	2.56
243 GRE	49	116	180	215	241	257	Trace	21	118	314	461	996	.008	.18	.65	1.46	1.92	3.77
245 SPA	54	136	198	238	262	295	Trace	30	139	261	420	743	.004	.21	.81	1.10	1.60	2.55
$LSD_{.05}$	7	18	17	23	22	38	1	13	48	73	111	160	.023	.10	.31	.36	.58	.81
$LSD_{.01}$	10	25	23	30	30	51	2	18	65	98	149	215	.037	.14	.42	.49	.78	1.10

(a) SWEden, SIBeria, CZEchoslovakia, GERmany, FRAnce, GREece, SPAin.

Figure 14. Root growth of eight seed sources of Scotch pine grown 80 days in the greenhouse.

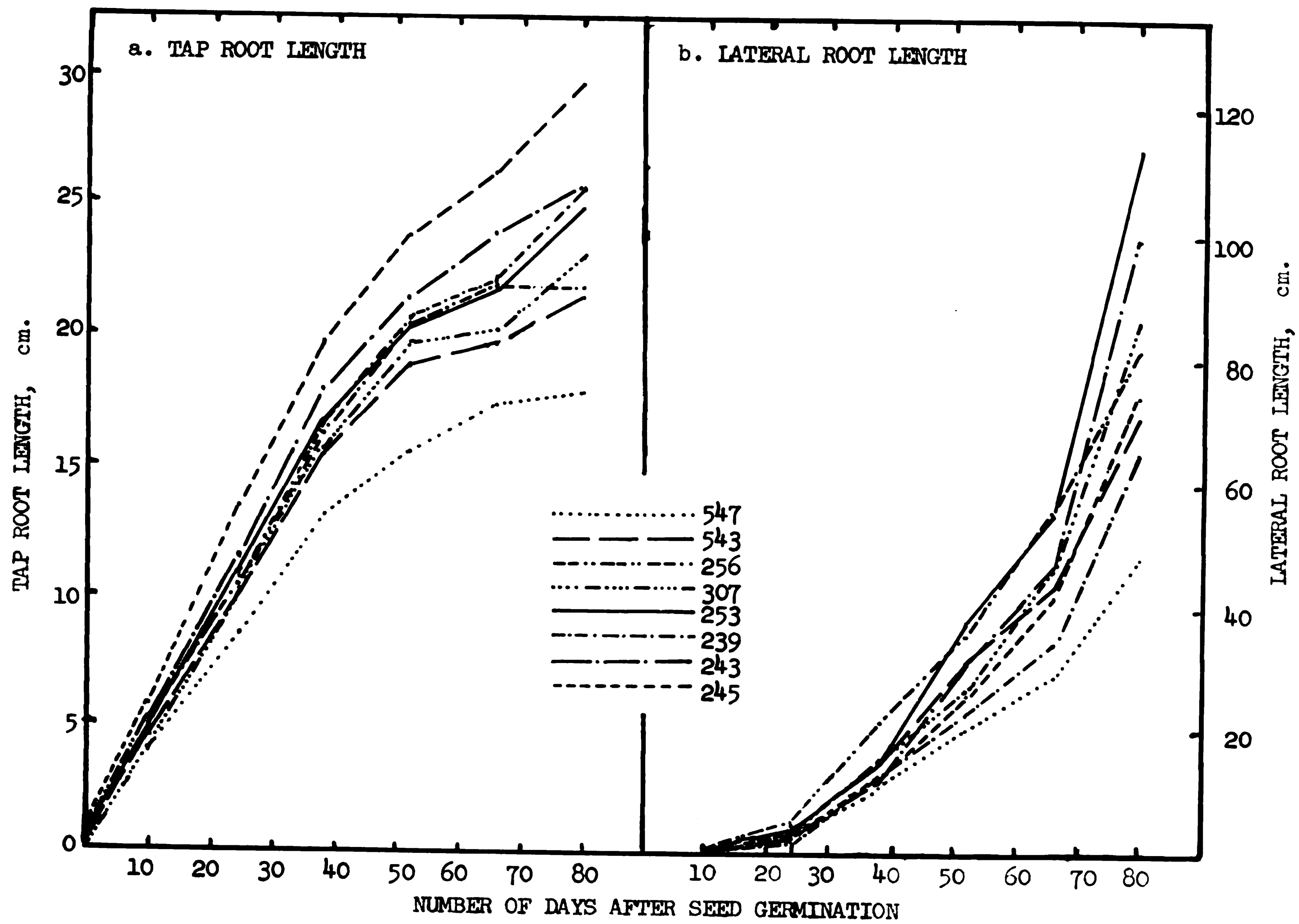

a. TAP ROOT LENGTH
b. LATERAL ROOT LENGTH
TAP ROOT LENGTH, cm.
LATERAL ROOT LENGTH, cm.
NUMBER OF DAYS AFTER SEED GERMINATION
0
5
10
15
20
25
30
20
40
60
80
100
120
10
20
30
40
50
60
70
80
547
543
256
307
253
239
243
245

Table 10. Dry weight of roots and relative dry weights of tap roots of Scotch pine provenances measured at 14-day intervals (a).

Seedlot, Country of Origin(b)	Total Root Weight at Age 10 days	24 days	38 days	52 days	66 days	80 days	Tap Root Weight as percent of total root weight at day: 52	66	80	Tap Root Weight per unit of length at day: 52	66	80
	---------milligrams----------						---% of total--			--mg./meter---		
Northern Origins												
547 SWE	1	3	4	8	10	15	69	43	40	36	34	34
543 SWE	1	3	7	12	14	22	61	47	42	38	34	42
256 SIB	1	3	10	15	21	29	53	43	37	38	40	49
Central European Origins												
307 CZE	1	3	7	11	16	26	60	51	43	33	42	48
253 GER	1	3	7	14	22	31	61	46	38	49	46	48
Southern Origins												
239 FRA	1	3	8	12	15	25	68	58	43	40	40	53
243 GRE	1	4	9	15	19	31	60	58	41	42	47	50
245 SPA	2	7	17	25	32	44	75	60	58	78	77	88
$LSD_{.05}$	.3	1.1	2.2	3.0	4.7	5.3	8	16	15	4	10	11
$LSD_{.01}$	.4	1.5	3.0	4.0	6.3	7.2	12	21	18	5	14	15

(a) Tap roots and lateral roots were not separated during weighings at days 10, 24, and 38.

(b) SWEden, SIBeria, CZEchoslovakia, GERmany, FRAnce, GREece, SPAin.

Lateral root elongation also started early in the northern origins. They exhibited the highest percentages of maximum lateral elongation at ages 24 to 66 days (Tables 9, 11). This characteristic was also very pronounced in MSFG 256.

The northern provenances had another distinctive trait. Most of the lateral roots grew from the upper portions of the tap root (Figures 15 - 17).

Central European Provenances. The central European provenances used were MSFG 253 from western West Germany and MSFG 307 from Czechoslovakia. Their rates of tap root and lateral root growth (expressed as a percent of the maximum attained during the study) were consistently less than those of northern sources. However, the ultimate lengths attained were greater for central European than for northern provenances.

The German and Czech origins had two characteristics in common to distinguish them from other sources. These were: the lateral roots were more branched than those of other sources (Table 12); and lateral roots grew from the entire tap root. Seedlings of MSFG 253 had the longest lateral roots, but only moderately long tap roots. The ratio of lateral to tap root length was greatest for seedlings of this source. The number of branched lateral roots in 80-day seedlings was significantly greater for this than for any other provenance.

The lateral roots of MSFG 307 were not so extensive as those of MSFG 253. The ratio of lateral to tap root length was approximately the same in the Czech source as in MSFG 243 from Greece and MSFG 256 from Siberia.

Table 11. Percentages of maximum (80-day) tap root and lateral root length attained at 14-day intervals in eight seed sources of Scotch pine.

Seedlot, Country of Origin(a)	Percent of maximum tap root length at age of						Percent of maximum lateral root length at age of					
	10 days	24 days	38 days	52 days	66 days	80 days	10 days	24 days	38 days	52 days	66 days	80 days
	percent						percent					
Northern Origins												
547 SWE	23	48	73	87	98	100	.1	6	23	42	60	100
543 SWE	20	46	71	87	92	100	.2	6	21	44	62	100
256 SIB	23	47	75	93	100	100	.3	5	26	43	67	100
Central European Origins												
307 CZE	18	44	68	85	87	100	.2	4	18	31	54	100
253 GER	19	44	67	82	88	100	.1	3	19	31	48	100
Southern Origins												
239 FRA	17	41	64	82	86	100	.1	3	19	35	53	100
243 GRE	19	45	70	81	85	100	Trace	2	12	31	46	100
245 SPA	18	46	67	81	90	100	Trace	5	19	35	56	100

(a) SWEden, SIBeria, CZEchoslovakia, GERmany, FRAnce, GREece, SPAin.

Figure 15. Root development of seedlings of MSFG 547 from north-central Sweden. Numbers below each seedling indicate the number of days after germination.

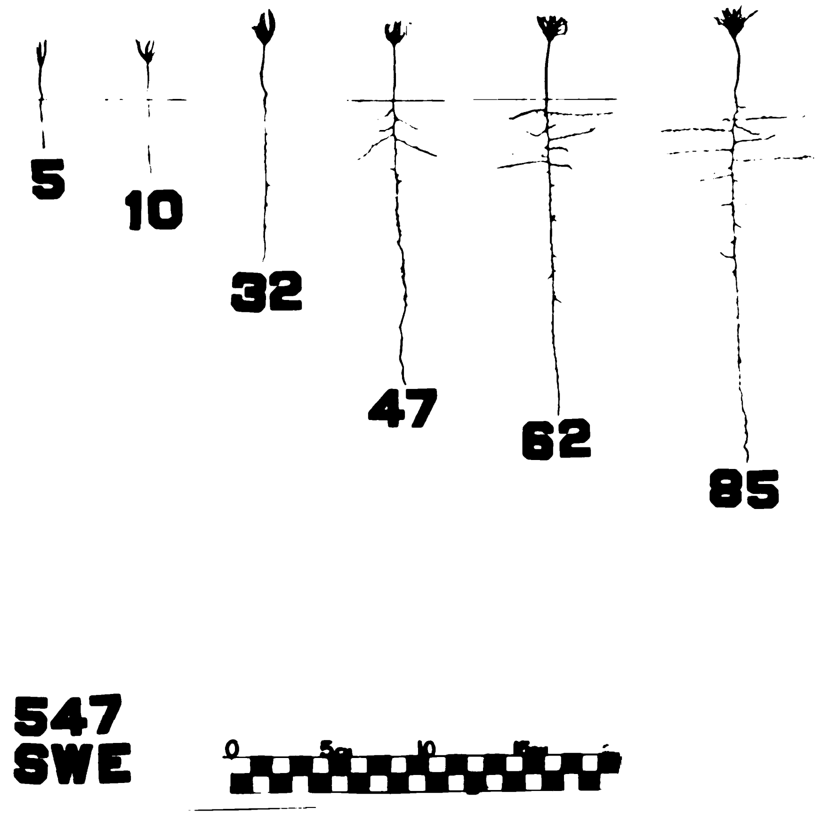


Figure 16. Root development of seedlings of MSFG 543 from south-central Sweden. Numbers below each seedling indicate the number of days after germination.

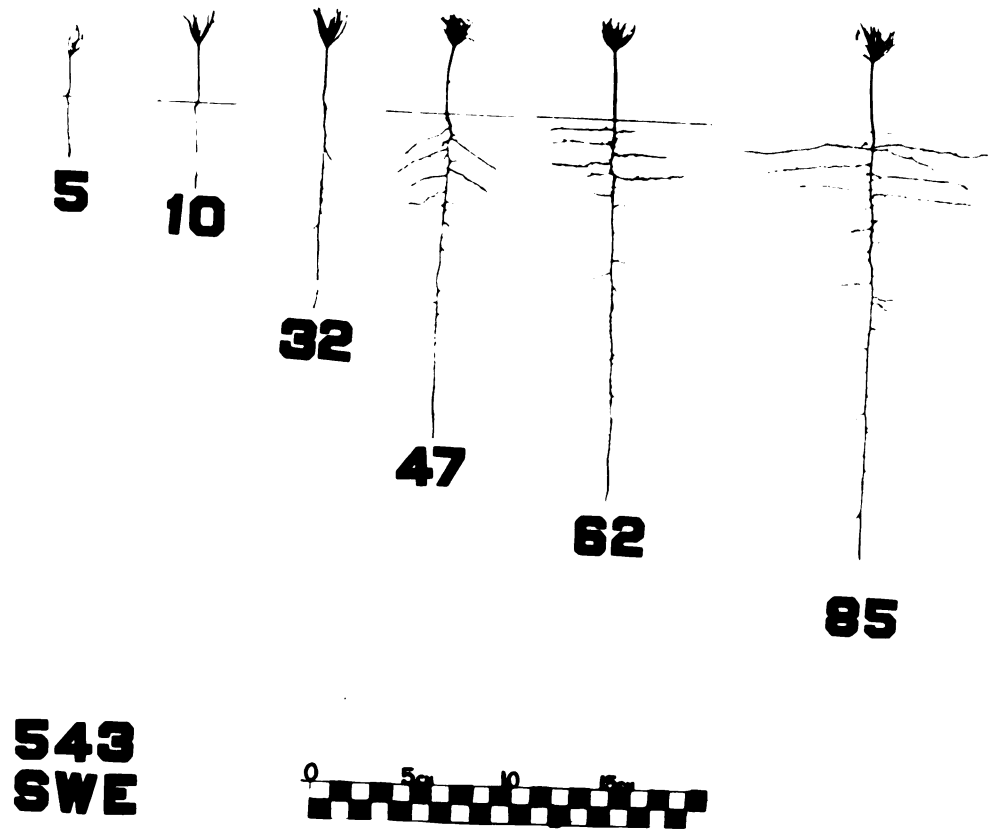


Figure 17. Root development of seedlings of MSFG 256 from central Siberia. Numbers below each seedling indicate the number of days after germination.

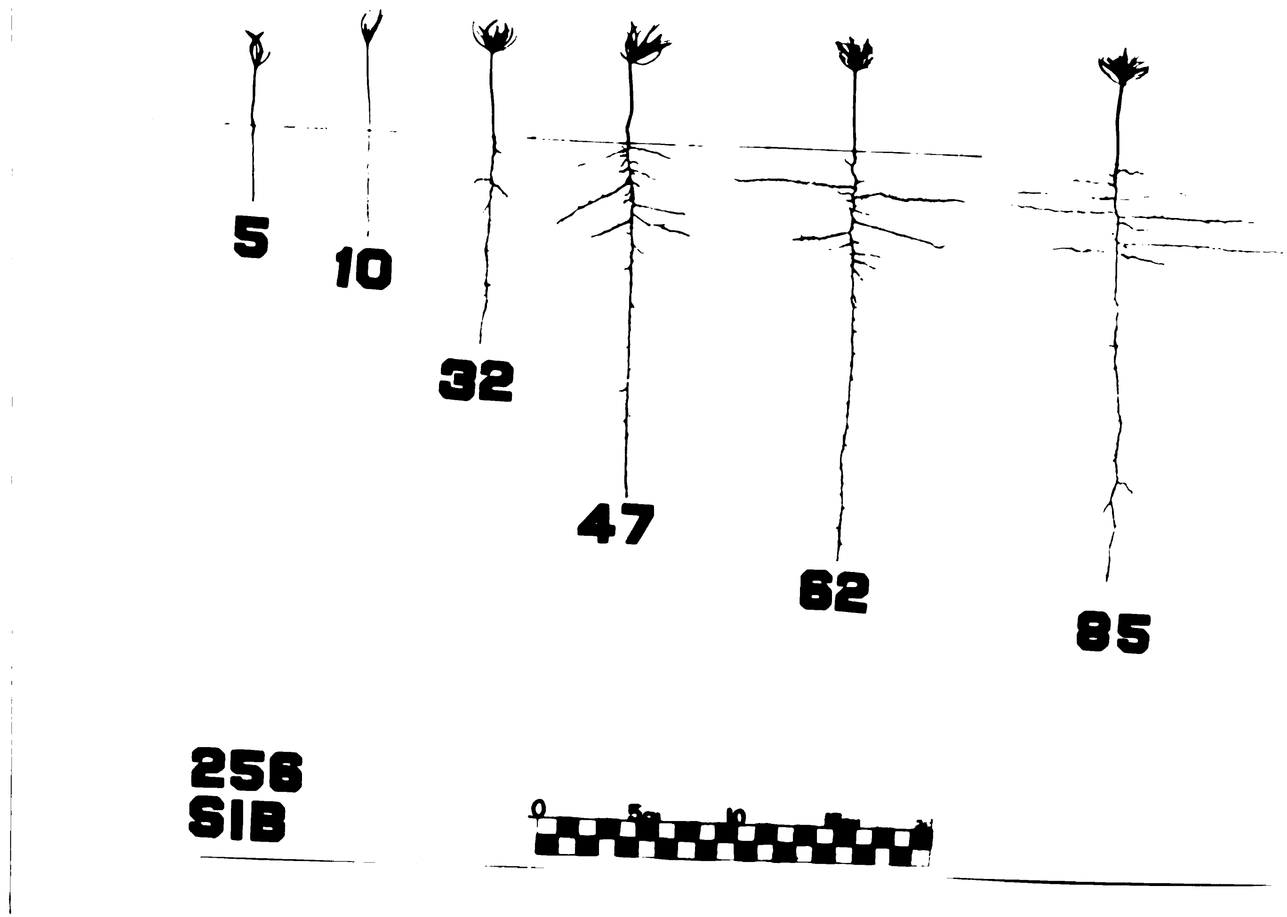


Table 12. Number of lateral roots per tree and proportion of lateral roots branched once or twice(a).

Seedlot, Country of Origin(b)	Lateral roots per tree at age 10 days	24 days	38 days	52 days	66 days	80 days	Proportion of laterals branched Once 38 days	52 days	66 days	80 days	Twice 66 days	80 days
	number						percent				percent	
Northern Origins												
547 SWE	1	20	53	102	136	192	6	6	5	5	0	1
543 SWE	2	22	71	150	206	288	7	4	5	5	0	1
256 SIB	3	25	94	155	231	329	8	5	5	5	Trace	1
Central European Origins												
307 CZE	2	24	75	136	216	305	6	6	6	5	Trace	2
253 GER	2	28	83	166	258	395	6	7	6	5	1	2
Southern Origins												
239 FRA	1	21	68	131	197	266	8	7	5	5	0	Trace
243 GRE	1	19	71	138	202	325	6	6	6	5	Trace	1
245 SPA	Trace	17	88	134	176	263	5	8	7	7	0	1
$LSD_{.05}$	1.6	7.3	22	31	34	49	-	-	-	-	-	-
$LSD_{.01}$	2.3	9.8	30	42	46	65	-	-	-	-	-	-

(a) Through the 24th day all laterals were unbranched. Remainder of lateral roots (to total of 100 percent) were unbranched.

(b) SWEden, SIBeria, CZEchoslovakia, GERmany, FRAnce, GREece, SPAin.

Figure 18. Root development of seedlings of MSFG 307 from Czechoslovakia. Numbers below each seedling indicate the number of days after germination.

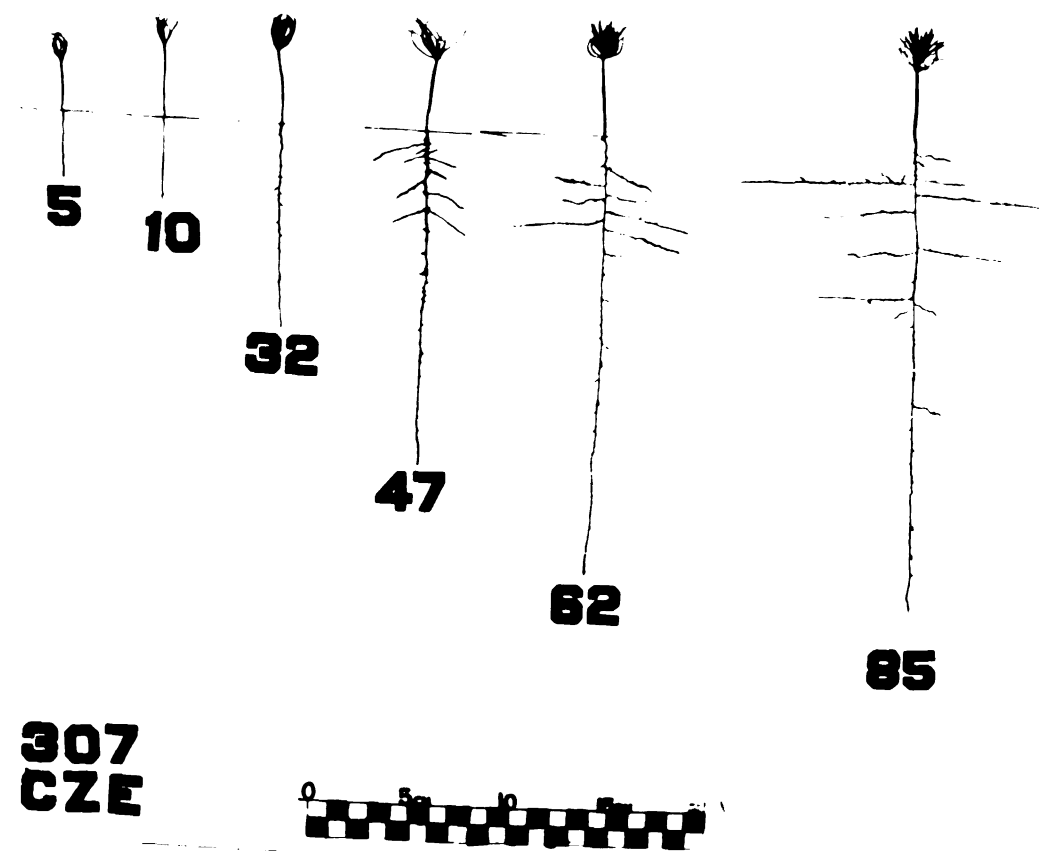
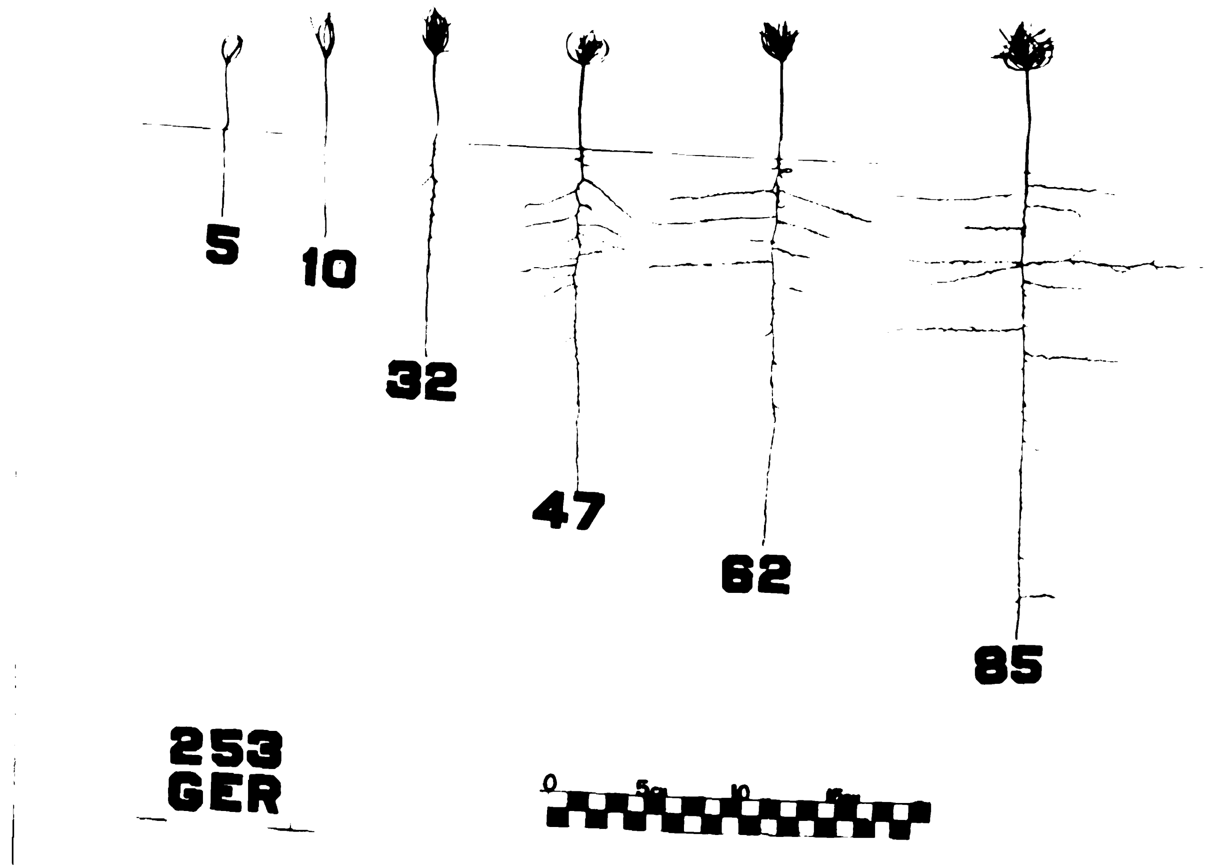


Figure 19. Root development of seedlings of MSFG 253 from western West Germany. Numbers below each seedling indicate the number of days after germination.



Southern Provenances. The three southern provenances were collected from stands in isolated portions of the Scotch pine range. MSFG 239 came from the Central Massif of France; 245 from the mountains of Spain; and 243 from the mountains of Greece. In type of root system these origins varied from more northern sources and from each other. They had three characteristics in common: long tap roots; relatively little branched lateral root systems (Table 12); and a significantly low ratio of lateral root to tap root length (Table 9).

Seedlings of MSFG 239 resembled northern trees in some ways. Tap roots were pronounced and laterals confined principally to the upper portion of the tap root (Figure 20). Rate of growth of tap and lateral roots (as a percent of the maximum) was slower than for northern origins. In fact, tap root development was slower for 239 than for any other source up until the 52nd day.

Seedlings of MSFG 245 had the longest and heaviest tap roots of all sources. This was true at all sampling times. Rate of tap root extension (as a percent of the maximum) was approximately the same as for the Greek, German and Czech sources, but was slower than that for the northern origins (Table 11). The weight per unit length of the tap roots of MSFG 245 was nearly double that of any of the other seven provenances (Table 10). Lateral root lengths of seedlings of MSFG 245 was moderate and occurred as relatively short extensions along much of the tap root. The root systems of Spanish No. 245 assumed a narrow, columnar appearance (Figure 21).

Rate of lateral root growth was slower for Greek MSFG 243 than any other origin despite the fact that total lateral length after 80 days was the second longest of all origins. Lateral extension occurred

Figure 20. Root development of seedlings of MSFG 239 from the Central Massif of France. Numbers below each seedling indicate the number of days after germination.

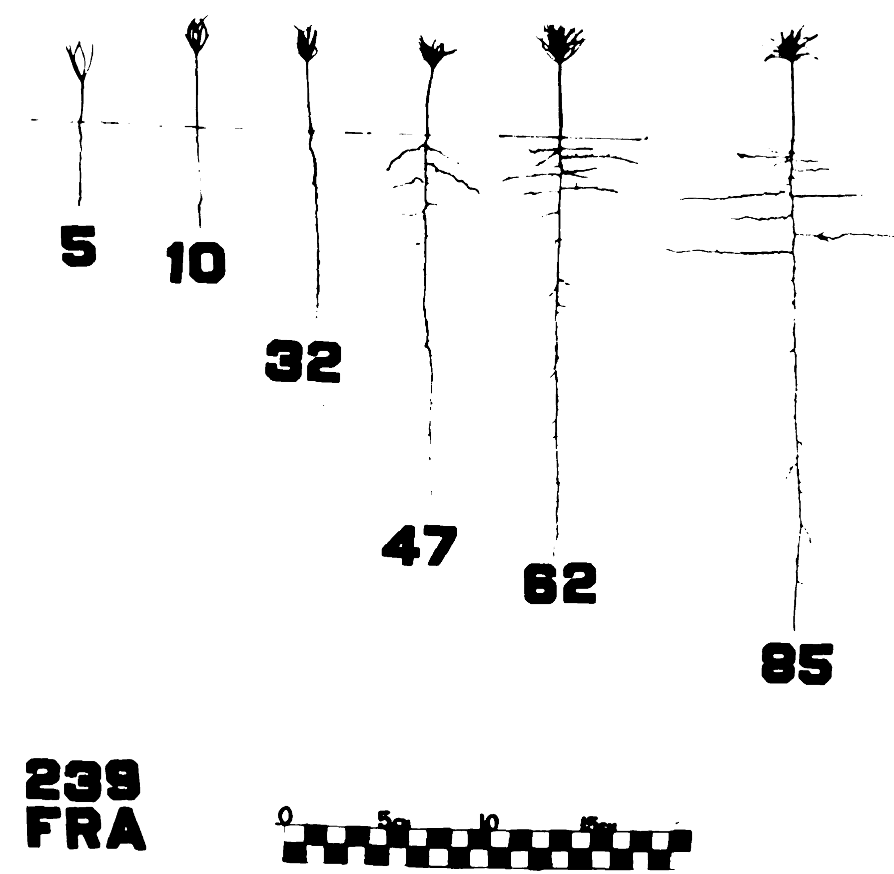
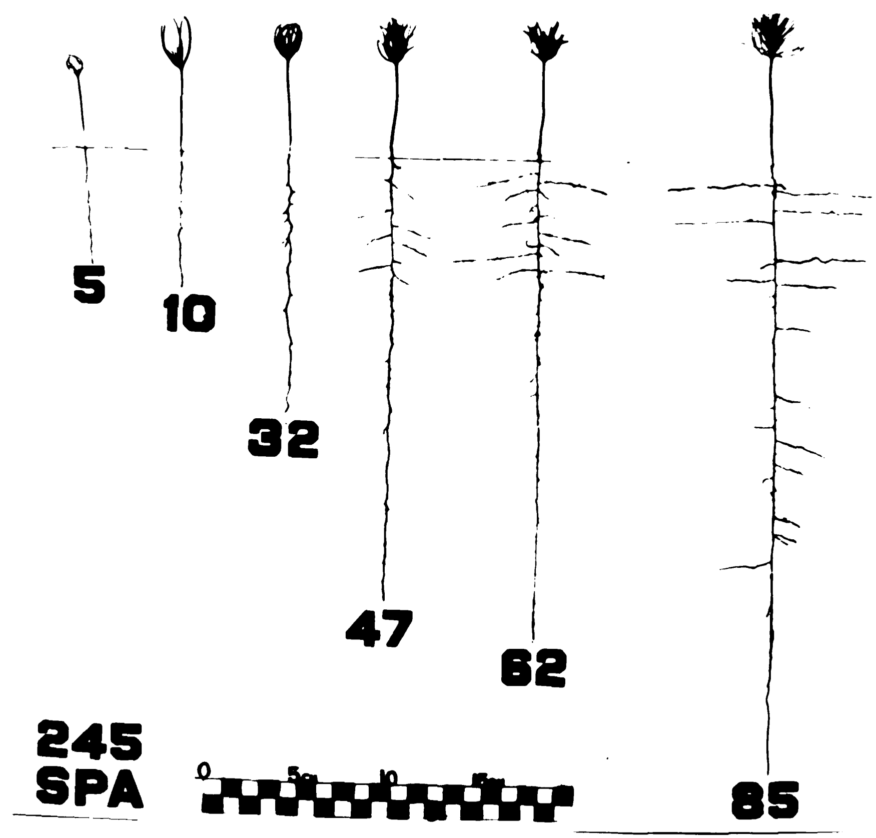
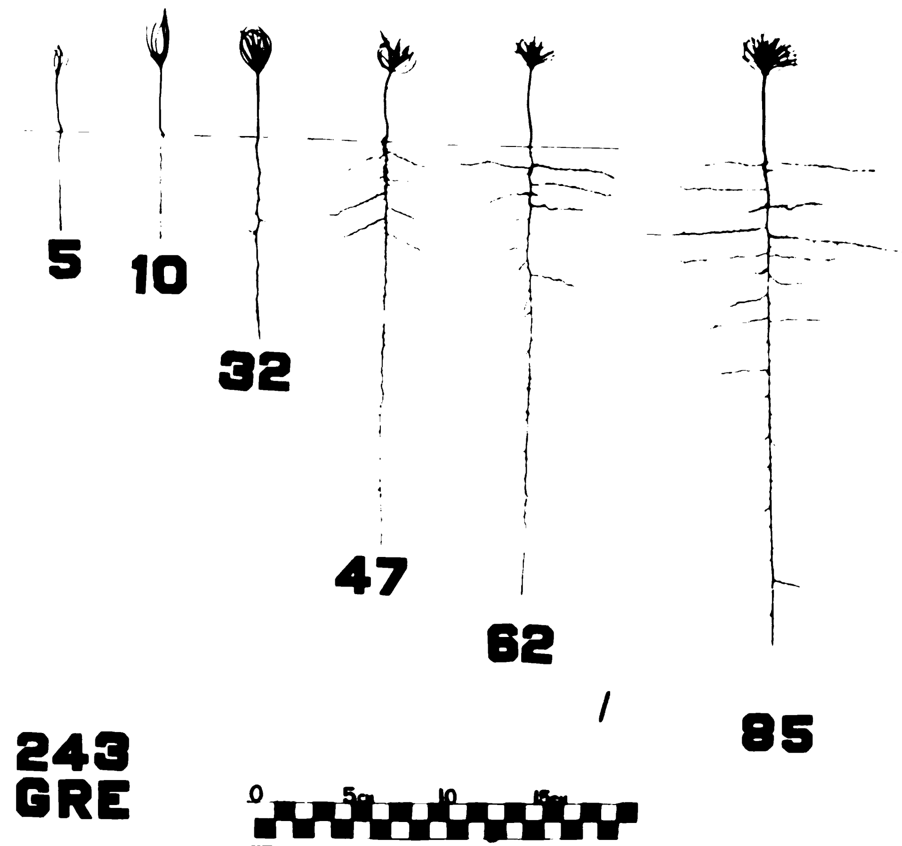


Figure 21. Root development of seedlings of MSFG 245 from the mountains of Spain. Numbers below each seedling indicate the number of days after germination.



along much of the tap root of seedlings of 243 and individual lateral roots were not so restricted in length as in MSFG 245 (Figure 22). The rate of tap root growth of 243 was not so slow as that for lateral root growth. It was approximately the same as that of the Spanish, German and Czech origins, but was slower than that of the northern provenances.

Figure 22. Root development of seedlings of MSFG 243 from the mountains of Greece. Numbers below each seedling indicate the number of days after germination.



RELATION OF ROOT TYPES AND GROWTH PATTERNS TO CLIMATE OF AREA OF ORIGIN

The rapid rate of root elongation of the northern provenances is probably related to low temperatures in the areas of seed collection. Temperatures were lower for the three northern areas than those of the locations from which the other five seed sources were collected (Table 7). The length of time during which growth would occur in the northern areas was also less than that for the other regions. Average monthly temperatures were above freezing for five, seven, and eight months, respectively, in the areas of origin of 256, 547, and 543; they were above 6^{o} C. for five, five, and six months, respectively. The rapid rate of root growth of the northern origins would enable seedlings to make maximum use of the limited period when temperatures would be favorable for growth.

Variations in rates of root growth of the three northern provenances seem to further substantiate this conclusion. Percentage rates of root extension were greatest for the Siberian provenance. The area from which this seed was collected also had the lowest average annual temperature and the shortest period when temperatures were above freezing. MSFG 547 had the second fastest rate of root growth and was collected from the area having the second coldest climate. MSFG 543, with the third fastest growth rate, came from the third coldest area of seed collection.

Root types of northern origins also appear to reflect the cold environments in which they evolved. Lateral root extension was concentrated near the top of the tap root. This could be an adaptive

character related to permafrost or relatively low temperatures at shallow depths in the soils of the areas of seed collection.

Root development of seedlings of Spanish 245 also appear to be related to climatic factors in the area of seed collection. Moisture, rather than temperature, was probably the factor governing development of the distinctive root type of this provenance. The region of origin is relatively dry and warm (Table 7). Total precipitation during the year averages slightly over 500 millimeters and growing season rainfall is only about half this amount. Precipitation during the growing season (April-September) is low and in August it averages less than 20 millimeters. Temperatures were the highest of all areas of seed collection. The growing-season aridity index, which is a measure of effective precipitation, is lowest in Spain. Soil moisture loss would be great under such conditions. Rapid and deep penetration of the tap root, with extension of laterals along much of its length, would be particularly beneficial adaptive characters for the establishment, survival and growth of seedlings.

Root development of the other four provenances could not be correlated with climatic data for the regions of seed collection. This possibly indicates that climate is not particularly critical. Average temperatures were not extreme: average annual temperatures ranged from 7.4° C. for the Greek provenance to 9.5° C. for the West German area and growing season temperatures ranged from 12.7° C. to 15.5° C. Precipitation did not appear to be limiting either. Growing season rainfall ranged from 338 millimeters for the West German source to nearly 1200 millimeters for the Greek origin. There were no months when precipitation was critically low and averages were generally

50 millimeters or greater per month. Aridity index values appeared to be favorable for all sources.

No clues could be found in the weather data as to why percentage rates of root elongation were unusually low for tap roots of French 239 and lateral roots of Greek 243. Precipitation-temperature data for the areas indicate very moist conditions. The aridity index for the Greek area was the highest of all areas of seed collection and that for the French area was second.

CHAPTER V

EFFECT OF AGE AND ROOT PRUNING ON ROOT DEVELOPMENT OF SCOTCH PINE SEEDLINGS OF DIFFERENT PROVENANCES

Numerous studies have noted variations in survival of tree species when transplanted at different times of the year. In general, these have shown that survival is lowest when transplanting is done during the period when top growth is most active. Drought has been given as the major cause of seedling mortality and this has been related to the inability of seedling root systems to supply moisture as rapidly as it is lost from the tops. This is caused, in part, by greater use and loss of water during the period when height growth is most active (Kramer, 1932 and 1943; Kozlowski, 1943; Gibbs, 1958).

It has also been shown that regeneration of new roots following transplanting varies with time of year. It is apparently greatest in late fall after top growth is completed and in early spring before top growth commences and is lowest during the spring and summer months when top growth is taking place (Neff and O'Rourke, 1951; Wilcox, 1955; Stone, 1955; Stone et al., 1959a, 1959b, 1962, 1963).

PROCEDURE

For this study, five seed sources of Scotch pine were selected, representing a north-south gradient through western Europe (Table 13). These sources are identical with those of the same MSFG number reported by Bull, Ruby, Wright, King, and various other NC-51 members (Wright and Bull, 1963; Ruby, 1964; King, 1965a and 1965b; Wright et al., 1966). Seed was sown in the Michigan State University Forest Research Center Nursery at East Lansing, Michigan in May 1965 using a randomized complete block design with four replications.

On July 20, approximately one month after germination, six seedlings from each seed source in each replicate were lifted from the nursery beds without visible damage to any roots. Two seedlings from each seed source and replicate were then subjected to one of three intensities of root pruning. These three were: removal of all lateral roots over three millimeters in length; removal of half of the lateral root system; and removal of no roots.

After root-pruning, each seedling was transplanted into an individual container and the roots were covered with a potting mixture consisting of two-thirds (by volume) 20 to 40 mesh quartz sand and one-third shredded peat moss. This mixture contained complete fertilizer sufficient to provide 50ppm each of N, P_2O_5, and K_2O. The seedlings were then placed in a greenhouse in the same order as in the nursery beds.

The seedlings were grown in the greenhouse for 30 days. They were watered at intervals to maintain moisture at a level slightly below field capacity. The trees were then removed from the pots and

Table 13. Location and climate at place of origin of Scotch pine seed sources used in transplanting study.

MSFG No. and Country of Origin (a)	Location Lat. N	Long. E	Elev.	Average Annual Temp.	Months Above 6° C.	Annual Precip.
	°	°	feet	°C.	No.	mm.
218 SPAin	40.0	-5.3	3700	10.0	7	366
240 FRAnce	42.6	2.1	4700	5.9	6	799
251 GERmany	49.1	8.1	500	9.9	7	536
550 SWEden	55.9	14.1	100	6.9	6	468
548 SWEden	63.5	18.7	700	2.0	4	568

(a) Numbers are those used in the Michigan State Forest Genetics accession record.

the root systems were carefully washed. Measurements were then made on survival, top length, total lateral root length, and absorbing lateral root length (Tables 14 and 17). The latter was defined as the white or unsuberized portion of the lateral root system and was also approximately equal to the amount of root elongation which occurred during the 30 day period when seedlings were in the greenhouse.

This procedure was repeated at monthly intervals until November 20, when the final (fifth) transplanting was made. The entire study therefore used a split-split plot experimental design, with time of transplanting as the main effect, the seed sources as the sub-plot effect, and intensity of root pruning as the sub-sub-plot effect, with 2-tree plots replicated four times.

Two variables, survival and absorbing lateral length, were considered of primary importance because they were affected most by the transplanting. The other two factors, total lateral root length and top length, were measured because they indicated stage of seedling development at time of transplanting.

Complete statistical analyses were made for three of the variables measured, survival, top length, and absorbing lateral root length (Table 15). Analyses of total lateral root length were made only for seedlings transplanted in September, October and November with no root-pruning (Table 18). High mortality after July and August transplantings resulted in many missing plots. Statistical analyses of the fifth variable studied $\left(\frac{\text{length of absorbing lateral roots}}{\text{total lateral root length}}\right)$ were confined to seedlings which had received no or half root pruning and which had been transplanted in September or later (Table 18). Analyses of root-shoot ratios were made for $\frac{\text{total lateral length}}{\text{shoot length}}$

for trees with no root pruning and for $\frac{\text{absorbing lateral length}}{\text{shoot length}}$ for trees with no, half and full root pruning (Table 20).

RESULTS

Survival

Survival varied significantly due to time of transplanting, seed source, and treatment (Tables 14, 15). Survival was low for all trees transplanted in mid-summer, especially for those which suffered the most drastic root pruning. It was moderately high for trees transplanted in September and nearly 100 percent for trees transplanted later. The differences between August, September, and October transplantings were statistically significant (1 percent level).

There were significant (1 percent level) time-seed source interactions. The three most southerly origins (MSFG 218, 240 and 251) had very low survival after transplantings in July and August and achieved 100 percent survival only after November transplantings. The two Swedish origins (MSFG 548 and 550) had appreciably better survival in midsummer and reached 100 percent survival after October lifting.

When seed sources were considered independently of time of transplanting, MSFG 548 had significantly more (67 percent) living trees than other sources. MSFG 550, also from Sweden, had the next highest survival (57 percent). Average survival of the three southern sources was 46 to 47 percent.

The effects of transplanting on survival also varied with intensity of root pruning. Removal of all the lateral roots gave significantly lower survival than did treatments which removed none and one-half of the lateral root systems. Treatment-seed source interactions were not significant, but treatment-time interactions were. Trees having no or one-half root removal had low survival from July and August

Table 14. Survival and height of Scotch pine seed sources one month after transplanting with various intensities of root pruning.

Date of Lifting	MSFG No. (a)	Survival after removal of the following portion of lateral roots present at the time of lifting			Height(b)
		None	Half	All	
		percent			mm.
July 20	218 SPA	12	12	0	31
	240 FRA	12	12	0	26
	251 GER	0	12	0	31
	550 SWE	25	12	0	30
	548 SWE	25	12	0	29
Aug. 20	218 SPA	12	12	0	55
	240 FRA	0	12	0	47
	251 GER	12	0	0	63
	550 SWE	38	25	0	54
	548 SWE	50	38	12	44
Sept. 20	218 SPA	62	75	0	72
	240 FRA	50	62	0	60
	251 GER	50	62	0	101
	550 SWE	75	75	0	70
	548 SWE	100	100	62	53
Oct. 20	218 SPA	100	100	25	70
	240 FRA	100	100	50	61
	251 GER	100	100	62	100
	550 SWE	100	100	100	71
	548 SWE	100	100	100	51
Nov. 20	218 SPA	100	100	88	71
	240 FRA	100	100	100	62
	251 GER	100	100	100	100
	550 SWE	100	100	100	70
	548 SWE	100	100	100	53

(a) SPAin, FRAnce, GERmany, SWEden

(b) Amount of root pruning did not affect height growth significantly.

transplantings. In later liftings the number of living trees increased, reaching 100 percent in October and November. For trees having full root pruning, there was no survival (except for MSFG 548) until after the October transplanting.

Table 15. Analyses of variance for survival, height, and length of absorbing portions of lateral roots of Scotch pine seed sources one month after transplanting with various intensities of root pruning.

Source of variation	Degrees of freedom	F ratios for Survival	F ratios for Height	F ratios for Length of absorbing lateral roots
Replication	3	--	--	--
Date of lifting	4	572.0***	370.6***	394.1***
Error a	12	--	--	--
Seed Source	4	13.8***	409.3***	141.0***
Source x Date	16	3.0***	32.9***	45.5***
Error b	60	--	--	--
Treatment	2	59.8***	2.9	355.5***
Treatment x Date	8	7.8***	.5	70.2***
Treatment x Source	8	1.6	.2	21.8***
Treatment x Date x Source	32	1.4	.4	6.7***
Error c	150	--	--	--

*** Significant at 0.1 percent level.

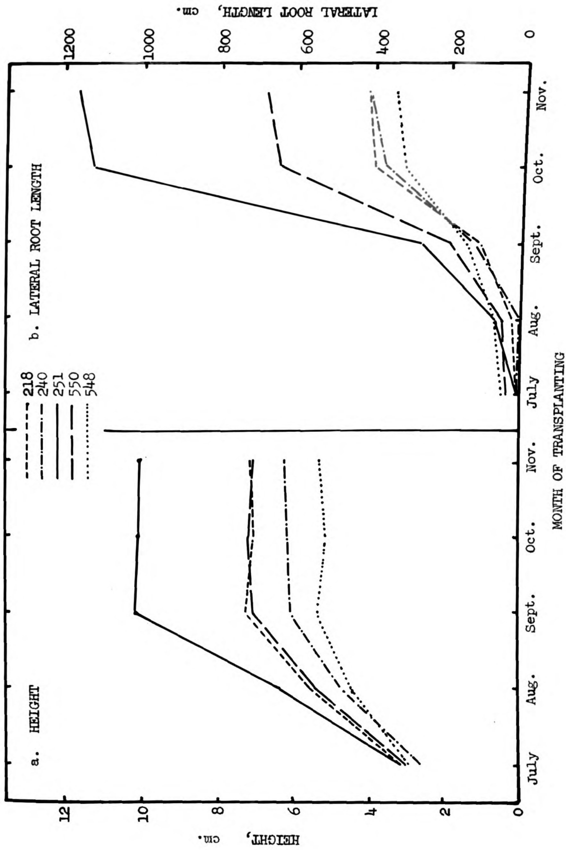
Top Growth

Most top growth occurred before transplanting. Therefore, it was affected significantly by time of measurement, seed source, and time-seed source interaction, but not by intensity of root pruning (Tables 14, 15).

In all five seed sources top growth was completed by September 20. As shown in Figure 23 and Table 14, MSFG 251 from Germany had a relatively rapid and constant growth rate throughout the growth period. Approximately one-third of the total elongation occurred between June and July, July and August, and August and September. MSFG 548 from northern Sweden had a decidedly different pattern. Over one-half of the total growth was completed by July 20 and over 80 percent was completed by August 20. Growth patterns of the other three sources were similar, with 43 percent of total elongation completed by July 20 and approximately 75 percent completed by August 20.

Seedlings of German 251 grew 100 mm. tall, nearly 30 mm. more than the next best sources, Spanish 218 and south-Swedish 550. Total top growth for south-French 240 was about 60 mm., while the maximum attained by north-Swedish 548 was a little over 50 mm..

Figure 23. Height and total lateral root length for five seed sources of Scotch pine transplanted with no root pruning at five different times.



a. HEIGHT
b. LATERAL ROOT LENGTH
218
240
251
550
548
HEIGHT, cm.
LATERAL ROOT LENGTH, cm.
MONTH OF TRANSPLANTING
July
Aug.
Sept.
Oct.
Nov.
0
2
4
6
8
10
12
200
400
600
800
1000
1200

Table 16. Percentage of end-of-season growth attained at various measurement dates (30 days after lifting dates).

MSFG No. (a)	Lifting Date	Height	Total length of lateral roots (Applies to trees with no lateral roots removed)	Length of absorbing roots after removal of following portion of lateral roots at lifting time		
				None	Half	All
		------Percent of end-of-season growth------				
218 SPA	July 20	43	1	1	2	--
	Aug. 20	76	5	9	6	--
	Sept. 20	100	26	39	60	--
	Oct. 20	100	95	100	100	94
	Nov. 20	100	100	100	100	100
240 FRA	July 20	43	1	4	0	--
	Aug. 20	76	--	--	6	--
	Sept. 20	100	31	36	47	--
	Oct. 20	100	89	88	90	86
	Nov. 20	100	100	100	100	100
251 GER	July 20	31	--	--	1	--
	Aug. 20	63	6	6	--	--
	Sept. 20	100	23	33	22	--
	Oct. 20	100	97	100	96	100
	Nov. 20	100	100	100	100	100
550 SWE	July 20	43	5	4	1	--
	Aug. 20	78	7	7	5	--
	Sept. 20	100	27	34	37	--
	Oct. 20	100	94	98	98	100
	Nov. 20	100	100	100	100	100
548 SWE	July 20	53	13	15	13	--
	Aug. 20	83	18	31	25	38
	Sept. 20	100	41	52	50	82
	Oct. 20	100	89	98	98	100
	Nov. 20	100	100	100	100	100

(a) SPAin, FRAnce, GERmany, SWEden.

Total Lateral Root Length

Only data for those trees which received no root-pruning and were transplanted from September to November were analyzed statistically. Differences due to time of transplanting, seed source, and time-seed source interaction were significant. The growth pattern was very different from that for top growth. Root growth was very slow during early- to mid-summer when top growth was greatest, but root growth continued much later than did top growth (Tables 17, 18).

Although data for July and August transplantings were not analyzed statistically, there were probably time-seed source interactions. After the first transplanting the two Swedish sources had the greatest total lateral root lengths. By the time of the August transplanting, the laterals on German 251 were about as long as on MSFG 548. After that the German source was constantly ahead. Spanish and French trees produced few lateral roots in the early months and did not catch up to the north Swedish trees until October.

The German seed source, MSFG 251, had a maximum total lateral root length of over 1100 cm., nearly 70 percent more than for Swedish 550, the source with the next longest lateral root length. MSFG 218 and 240 had total lateral lengths of about 400 cm., while trees of Swedish 548 attained a maximum lateral extent of 340 cm.

The significant time-seed source interaction can be attributed mainly to differences between September transplanted trees and those transplanted later (Tables 16, 18). Of trees transplanted in September, MSFG 251 had only about twice as long a lateral root system as MSFG 548. In contrast, after October and November transplantings

Table 17. Lateral root length of Scotch pine seed sources one month after transplanting with various intensities of root pruning.

Date of lifting	MSFG No.(a)	Lateral roots one month after removal of the following portions of laterals: Total Length			Absorb. Length			Ratio: Absorbing / Total Roots Removed		
		None	Half	All	None	Half	All	None	Half	All
		---------centimeters---------						---number----		
July 20	218 SPA	4	6	--	2	3	--	.38	.50	--
	240 FRA	5	1	--	5	1	--	1.00	1.00	--
	251 GER	--	4	--	--	2	--	--	.50	--
	550 SWE	32	2	--	8	2	--	.25	1.00	--
	548 SWE	44	21	--	10	13	--	.22	.62	--
Aug. 20	218 SPA	21	17	--	8	10	--	.40	.59	--
	240 FRA	--	19	--	--	10	--	--	.50	--
	251 GER	65	--	--	15	--	--	.23	--	--
	550 SWE	46	19	--	14	14	--	.29	.71	--
	548 SWE	63	38	15	20	24	15	.31	.63	1.00
Sept. 20	218 SPA	108	146	--	38	100	--	.36	.69	--
	240 FRA	125	115	--	49	80	--	.39	.70	--
	251 GER	264	149	--	88	89	--	.33	.59	--
	550 SWE	188	158	--	62	107	--	.34	.68	--
	548 SWE	142	82	27	32	48	26	.23	.59	.98
Oct. 20	218 SPA	393	360	30	100	168	27	.26	.47	.90
	240 FRA	362	319	50	92	152	43	.25	.48	.36
	251 GER	1125	878	98	265	390	90	.24	.44	.92
	550 SWE	642	599	59	178	282	55	.28	.47	.93
	548 SWE	308	228	44	60	95	40	.20	.42	.98
Nov. 20	218 SPA	414	332	50	98	155	46	.24	.48	.92
	240 FRA	408	338	34	103	170	50	.25	.50	.93
	251 GER	1162	900	90	256	405	86	.22	.50	.95
	550 SWE	685	580	58	181	288	53	.26	.50	.92
	548 SWE	345	226	40	62	97	38	.18	.43	.93

(a) SPAin, FRAnce, GERmany, SWEden

MSFG 251 had nearly four times as long lateral roots as did MSFG 548. The roots of October transplanted trees of all seed sources were 90 to 97 percent as long as on November-transplanted ones; there were no significant time-seed source interactions for these months. For individual months, ranking of total lateral lengths remained relatively constant for the different seed sources.

Table 18. Analyses of variance for total length of lateral roots and for the ratio $\frac{\text{absorbing}}{\text{total}}$ lateral root length of Scotch pine seed sources measured one month after transplanting at various dates (a).

Source of variation	Degrees of freedom	Total length of lateral roots	Ratio of $\frac{\text{Absorbing}}{\text{Total}}$ lateral root length
Replication	3	--	--
Date of lifting	2	105.3***	207.2***
Error a	6	--	--
Seed Source	4	89.3***	8.4***
Source x Date	8	12.6***	.3
Error b	36	--	--
Treatment	1	--	410.0***
Treatment x Date	2	--	7.0***
Treatment x Source	4	--	.4
Treatment x Date x Source	8	--	.1
Error c	45	--	--

(a) Due to high mortality after the July and August transplantings these variables were analyzed for only a portion of the data.

*** Significat at the 0.1 percent level.

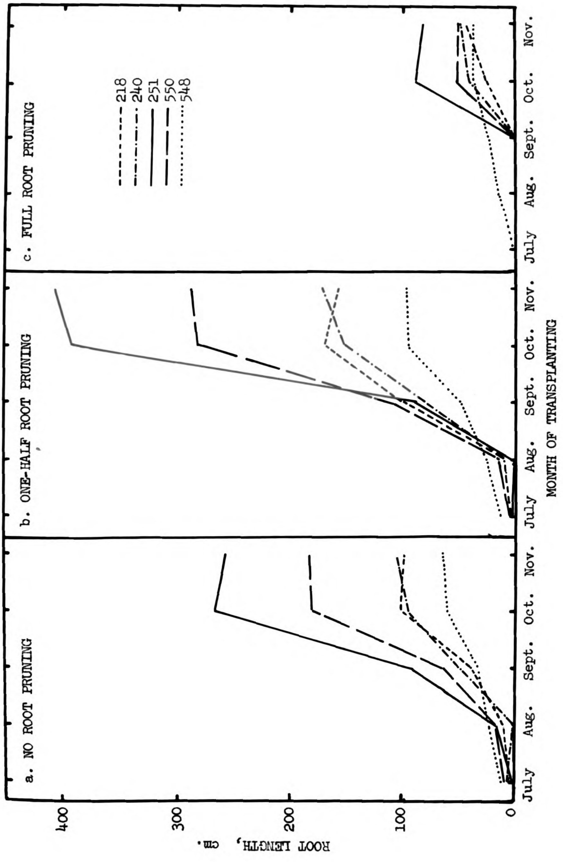
Absorbing Lateral Length

The "absorbing" (white) lateral roots were approximately equal to the amount of lateral root growth which took place during the 30 day period when seedlings were in the greenhouse. This new lateral growth originated from two sources: new growth on the tips of existing laterals present at the time of transplanting and new roots which originated near the ends of cut laterals. The majority of new growth on trees which received no root pruning was of the first type. Essentially all new root growth on root-pruned trees was of the second type.

There were significant differences in length of absorbing lateral roots due to date, seed source, and treatment (Figure 24). Also, all second- and third-order interactions were significant. There was very little new lateral root elongation on any source transplanted in July and August. Progressively greater amounts of new growth were associated with September and October transplanting. There was than a leveling off, with essentially the same amount of new growth after November transplantings as after those made in October. All monthly differences except the July-August and October-November comparisons were significant.

There were pronounced differences among sources in the total length of absorbing laterals produced by the end of the season (November). The German source, MSFG 251, had the greatest absorbing lateral root extent. South Swedish 550 had the next greatest amount and north Swedish 548 the least. For trees with no root pruning, MSFG 251 reached a maximum of approximately 250 cm. of absorbing lateral

Figure 24. Length of absorbing (white) roots of Scotch pine as affected by date of transplanting, intensity of root pruning at transplanting time and seed source.



a. NO ROOT PRUNING
b. ONE-HALF ROOT PRUNING
c. FULL ROOT PRUNING
218
240
251
550
548
ROOT LENGTH, cm.
0
100
200
300
400
July
Aug.
Sept.
Oct.
Nov.
MONTH OF TRANSPLANTING

length after October and November transplantings, compared with 180 cm. for MSFG 550, approximately 90 cm. for MSFG 240 and 218 and only about 50 cm. for MSFG 548. Averages for trees receiving half or full root pruning were different from these values, but ranking of seed sources was the same.

The ranking of seed sources also varied with transplanting date. North-Swedish 548 had the longest absorbing laterals after the July and August transplantings although it had the least amount of absorbing laterals from September on. Conversely, German 251 had intermediate absorbing lateral lengths after the first two transplantings, but had the greatest amount when trees were transplanted in September or later.

The pattern for absorbing lateral root length at different intensities of root pruning was very different from that described for survival. Whereas survival was approximately the same for trees with no or half root pruning, average length of absorbing laterals was significantly greater on trees having half root pruning. There were also noticeable differences in amount of new absorbing laterals associated with treatment after various transplanting dates. For trees transplanted in July and August, the length of absorbing laterals was nearly the same for trees which had lost half their laterals as for trees which had not been root-pruned. For trees transplanted in October and November, the length of absorbing laterals was approximately 50 percent greater if the trees had lost half their laterals than if no root pruning had been done. Another dissimilarity between absorbing lateral length and survival was in the size of the treatment-seed source interaction. The average absorbing lateral root length for half root-pruned trees of MSFG 251 and 548 was 45 percent greater than for unpruned trees. For MSFG 240 and 218 removal of half the laterals caused an increase of 75 percent in the amount of absorbing lateral length; for MSFG 550 the corresponding increase was 60 percent. Conversely, the reductions in absorbing lateral roots associated with complete removal of laterals was greatest for sources MSFG 218, 251 and 550 (75 percent), intermediate for MSFG 240 (60 percent) and least for MSFG 548 (40 percent).

Ratio: $\dfrac{\text{Absorbing Root Length}}{\text{Total Root Length}}$

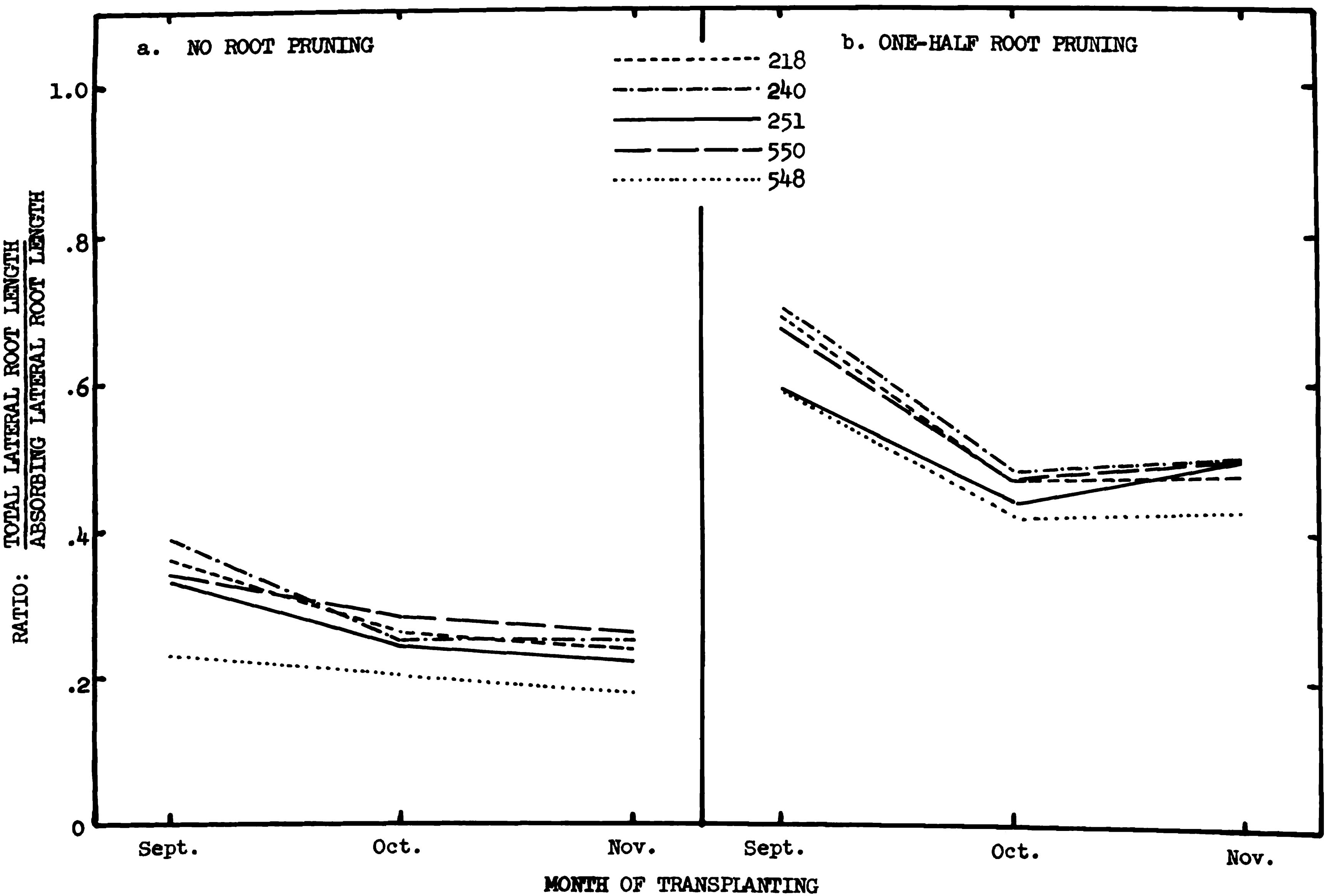
If the amount of new root development, or absorbing lateral length, which develops after transplanting is examined as a proportion of the total lateral root length, results are different than for the two variables considered independently. Although German 251 had the greatest absolute lengths for both total and absorbing laterals, this seed source produced significantly less relative absorbing surface than did MSFG 218, 240 and 550. MSFG 548, on the other hand, the source with the least total and absorbing lateral lengths, had the lowest relative absorbing lateral root surface. Although Swedish 550 had much greater total and absorbing lateral root lengths than MSFG 218 and 240, all three seed sources had nearly the same $\frac{\text{absorbing length}}{\text{total length}}$ ratios.

Also, the proportion of relative absorbing surface decreased constantly between the third transplanting in September and the fourth in October, despite the fact that absolute amounts of both total and absorbing lateral root lengths increased significantly during the same period. In other words, the amount of absorbing surface did not increase as fast as did total length. This pattern was similar for all sources and the time-seed source interaction was not significant (Figure 25, Table 17).

The effects of root pruning were also significant. Those trees which were half root-pruned had greater $\frac{\text{absorbing length}}{\text{total length}}$ ratios than did unpruned trees. Of course, practically all roots were white and apparently absorbing on trees from which all original roots were removed.

There was a significant date-treatment interaction. The decrease in relative $\frac{\text{absorbing length}}{\text{total length}}$ ratio from September to October transplantings was greater for half-pruned than for unpruned trees (Figure 25). This decrease in relative absorbing surface continued slightly from October to November for half-pruned trees, but unpruned trees retained about the same ratio.

Figure 25. Ratio of $\frac{\text{Absorbing}}{\text{Total}}$ lateral root length of Scotch pine transplanted from September through November and subjected to no or one-half root pruning.


a. NO ROOT PRUNING
b. ONE-HALF ROOT PRUNING
218
240
251
550
548
1.0
.8
.6
.4
.2
0
RATIO: TOTAL LATERAL ROOT LENGTH / ABSORBING LATERAL ROOT LENGTH
Sept.
Oct.
Nov.
Sept.
Oct.
Nov.
MONTH OF TRANSPLANTING

Root-Shoot Ratios

There were significant differences in root-shoot ratios due to date of transplanting, seed source and intensity of root pruning (Tables 19 and 20 and Figure 26). All second- and third-order interactions were also significant. Root-shoot ratios were low for all origins transplanted in July and August. There were then significant increases in root-shoot ratios after September and October transplantings, followed by a leveling off of ratios for seedlings which were transplanted in November.

The ranking of seed sources varied considerably with transplanting date. North Swedish MSFG 548 had the highest (most favorable) root-shoot ratios after July and August transplantings. By the time of the September lifting, ratios for the other sources generally equalled or exceeded those of MSFG 548. After October and November transplantings only those ratios for Spanish MSFG 218 which had been calculated using $\frac{\text{total lateral length}}{\text{top length}}$ were lower than the root-shoot ratios for MSFG 548.

There were pronounced differences among seed sources in root-shoot ratios at the last transplanting in November. Based on ratios of $\frac{\text{total lateral length}}{\text{top length}}$ German MSFG 251 had ratios which were nearly 20 percent greater than those of south-Swedish 550 and which were about twice as large as those for MSFG 240, 218 and 548. Final root-shoot ratios based on absorbing lateral lengths were somewhat different from those based on total lateral root lengths. MSFG 251 and 550 had ratios which were about equal and the ratios for these two sources were 150 to 225 percent greater than those for the other

Table 19. Root-shoot ratios of Scotch pine seed sources after transplanting with various intensities of root pruning.

Date of Lifting	MSFG No. (a)	Root-Shoot Ratio			
		Tot. Lat. Length / Shoot Length (No root pruning)	Absorbing Lateral Length / Shoot Length		
			No Root Pruning	Half Root Pruning	Full Root Pruning
July 20	218 SPA	1.33	0.50	0.92	--
	240 FRA	1.89	1.13	0.19	--
	251 GER	--	--	0.65	--
	550 SWE	9.64	2.41	0.36	--
	548 SWE	15.27	3.30	4.51	--
Aug. 20	218 SPA	3.85	1.56	1.75	--
	240 FRA	--	--	2.01	--
	251 GER	10.13	2.34	--	--
	550 SWE	8.14	2.40	2.59	--
	548 SWE	13.76	4.26	5.24	3.80
Sept. 20	218 SPA	14.75	5.20	13.85	--
	240 FRA	20.77	8.13	13.29	--
	251 GER	26.14	8.66	8.86	--
	550 SWE	27.72	9.22	14.81	--
	548 SWE	25.73	5.91	9.27	5.18
Oct. 20	218 SPA	55.51	14.12	23.76	3.87
	240 FRA	60.62	15.30	24.21	7.41
	251 GER	111.39	26.23	38.42	9.14
	550 SWE	89.48	24.72	40.24	8.11
	548 SWE	59.71	11.75	18.55	7.78
Nov. 20	218 SPA	58.47	13.77	21.99	6.52
	240 FRA	65.68	16.56	27.20	8.04
	251 GER	118.02	25.99	40.10	8.57
	550 SWE	98.14	25.93	40.61	7.57
	548 SWE	- 64.84	11.65	18.03	7.01

(a) SPAin, FRAnce, GERmany, SWEden

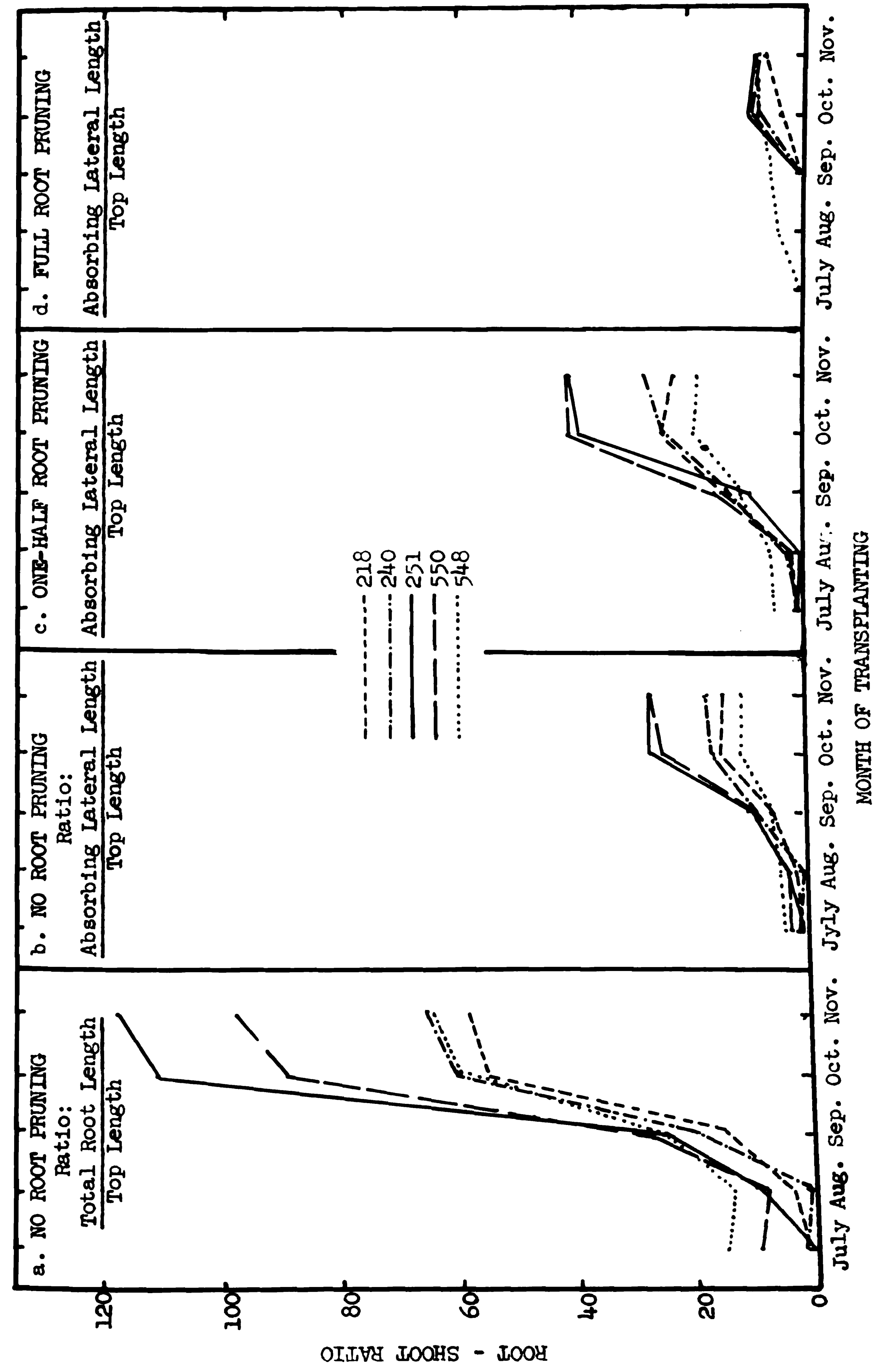
Table 20. Analyses of variance for root-shoot ratios of Scotch pine seed sources one month after transplanting with various intensities of root pruning.

Source of variation	Degrees of freedom	F ratios for: Tot. Lat. Length / Shoot Length(a)	Absorb. Lat. Length / Shoot Length
Replication	3	--	--
Date of Lifting	4	205.9***	607.3***
Error a	12	--	--
Seed Source	4	35.5***	40.4***
Source x Date	16	10.4***	16.7***
Error b	60	--	--
Treatment	2	--	344.8***
Treatment x Date	8	--	64.3***
Treatment x Source	8	--	9.6***
Treatment x Source x Date	32	--	3.4***
Error c	150	--	--

(a) Root-shoot ratios calculated using total lateral root lengths were analyzed only for those trees with no root pruning.

*** Significant at the 0.1 percent level.

Figure 26. Root-shoot ratios of five seed sources of Scotch pine as affected by transplanting date and intensity of root pruning.


a. NO ROOT PRUNING
Ratio:
Total Root Length
Top Length
b. NO ROOT PRUNING
Ratio:
Absorbing Lateral Length
Top Length
c. ONE-HALF ROOT PRUNING
Absorbing Lateral Length
Top Length
d. FULL ROOT PRUNING
Absorbing Lateral Length
Top Length
218
240
251
550
548
ROOT - SHOOT RATIO
0
20
40
60
80
100
120
July Aug. Sep. Oct. Nov.
Jyly Aug. Sep. Oct. Nov.
July Aug. Sep. Oct. Nov.
July Aug. Sep. Oct. Nov.
MONTH OF TRANSPLANTING

three origins.

Different intensities of root pruning also produced significant differences in ratios of $\frac{\text{absorbing lateral length}}{\text{top length}}$. After mid-summer transplantings, those ratios for trees with no and half root pruning were approximately the same. At the time of the September transplanting, ratios for half-root-pruned trees were higher and after October and November liftings root-shoot ratios for half-root-pruned trees were 55 to 60 percent greater than those of trees with no root pruning. Trees with full root pruning had root-shoot ratios which were significantly lower than for no and half-root-pruned trees. All sources with full root pruning had ratios which were about equal at the time of the last transplanting.

Relation of Top to Root Growth

During the period of most active height growth (July-September) root growth was relatively slight. It was not until after terminal shoot growth had slowed down or was completed that the majority of the root growth took place (Figure 23). Nearly half the total root elongation occurred during September and October on seedlings of MSFG 548. During that same period the proportion of total root growth achieved was approximately 60, 66, and 70 percent, respectively, for MSFG 240, 550 and 218. Fast growing German 251 had the highest percentage of total root growth during this interval; 72 percent of root elongation took place after the completion of height growth in September. These relationships can be stated statistically by correlations based on date-seedlot-treatment means for all five transplanting periods as items. The correlation coefficient between height and total lateral root length (for trees with no root pruning) was -0.87. Those between height and absorbing lateral roots were -0.85 and -0.82, respectively, for trees with no and half root pruning.

Similar trends in shoot versus root growth have been found in citrus and other fruit trees; Norway and Sitka spruce; European larch; red, white, Scotch, longleaf, slash, loblolly and shortleaf pines (Harris, 1929; Stevens, 1931; Laing, 1932; Kienholz, 1934; Turner, 1936; Huberman, 1940; Marloth, 1949; Reed and MacDougal, 1937). This inverse correlation between periods of active height and root growth is apparently associated with availability of manufactured carbohydrates. Growth of the Scotch pine seedlings used in this study was dependent initially on food materials stored in the seed, then on currently manufactured photosynthate, with little or none available for storage. Initially this photosynthate was used primarily for top growth. Kramer and Kozlowski (1960), reviewing earlier work, reported a tendency toward polarity in translocation of food in plants. Carbohydrates and other metabolites tend to move toward actively growing regions at the expense of more slowly growing regions, including root systems.

The cause of this apparent polarity in translocation is not fully understood. Kramer and Kozlowski felt that the level of auxin production partly controls the direction of translocation through its effects on metabolic activity.

Relation of Survival to Root Growth and Root-Shoot Ratios

Survival was closely correlated with the amount of roots present at transplanting, the growth of new roots after transplanting, and with root-shoot ratios of the seedlings. During the early part of the growing season root-shoot ratios were very low and neither the amount of roots present at transplanting nor the new growth after transplanting was sufficient to supply the moisture needed by the actively growing trees. Of the five seedlots transplanted during July and August only 548 from northern Sweden survived even moderately well and that was the origin with the largest root system at time of transplanting, the most root growth during the subsequent months and the most favorable root-shoot ratios (Tables 17 and 19).

Of the trees transplanted during September, those with half their root systems removed actually produced more absorbing roots during the subsequent month than did unpruned trees. Root-shoot ratios based on absorbing lateral lengths were higher for these half pruned trees than for those with no root pruning and they generally survived a little better. As transplanting was done later in the fall, the amount of lateral growth increased, height growth decreased and root-shoot ratios increased (Figures 23 and 26). Survival of trees transplanted in October and November was 100 percent for all trees which had no or half root pruning, although there was considerable variation in root-shoot ratios of seedlings. Trees with all laterals removed at transplanting time could produce relatively few new roots in the subsequent month and did not survive well except after the last transplanting.

Time of completion of height growth also apparently affected survival. Seedlot 548 from northern Sweden survived as well or better than all other sources after all treatments and times of transplantings although it had the most lateral roots and most favorable root-shoot ratios only during the early part of the season. The early completion of height growth of this source may have accounted for its good survival after later transplantings. Studies on other trees (reviewed by Kramer and Kozlowski, 1960) have shown that water metabolism and transpirational losses are greatest during the season of active height growth. This reduced water use and loss for MSFG 548 apparently counterbalanced its lower root-shoot ratios.

The same sources used in this study (and 103 others) were field planted during 1961 and 1962 at 31 locations in the north-central states as part of the NC 51 project (Wright _et al._, 1966). Two-year-old seedlings were used. The survival pattern differed somewhat from that reported here. Survival was poorest in sources from northern Scandinavian var. _lapponica_ (includes MSFG 548) and was best for var. _iberica_ from Spain (includes MSFG 218), var. _aquitana_ from southern France (includes MSFG 240), and var. _rigensis_ from southern Sweden (includes MSFG 550). Survival of sources from central Europe, including var. _haguenensis_ (includes MSFG 251), was also rather low. Differences in results between the two studies seem to be related to root-top ratios and to differences between field and greenhouse conditions.

In the earlier study north-Swedish seedlings had excellent but short root systems which apparently were incapable of penetrating the soil fast enough to keep ahead of surface drying which takes place in the open during the summer. Results from the study reported here also indicate that root-top balance of north-Swedish seedlings is unfavorable. After October and November transplanting, MSFG 548 had the lowest ratio of absorbing lateral root length to top length of the five origins used. It is also probable that if the seedlings used in the older study had been transplanted to greenhouse conditions where the soil was constantly moist that they would have shown very little transplanting shock and survival would have been good.

In the earlier study poor survival of 2-0 seedlings of central European origin was apparently related to unfavorable root-shoot balance of seedlings which had been grown in crowded nursery beds. Excellent survival was obtained from plantings of 2-1 seedlings of central European origin planted in Minnesota. The study reported here showed that seedlings of German 251 grown in uncrowded beds had excellent root-shoot ratios. This study also showed that root-shoot balance was very high for seedlings of south-Swedish 550. The high field survival of the Spanish trees was somewhat surprising in view of the low root regenerating ability and low root-shoot ratios shown by seedlings in my study.

E. C. Stone and his associates (Stone, 1955; Stone et al., 1959a, 1959b, 1962 and 1963) have studied seasonal variation in root regeneration of ponderosa pine and Douglas-fir. Trees transplanted in late spring and early summer had the lowest root regenerating potential and survival rates. Both increased gradually in early fall, sharply in late fall, and stayed constant until early spring. There were genetic differences in ponderosa pine, with high elevation sources having the most rapid rate of increase in root regeneration potential and survival percent in the autumn. This is similar to the trend found in my study in which seedlots from the coolest climates developed the highest survival potential earliest in the season.

Nurserymen have practiced partial root pruning for many years, usually doing this one year prior to field planting on the theory that new laterals would develop during the ensuing season. This is undoubtedly good practice. Extensive root pruning at the time of field planting has not been generally recommended unless root systems are unusually large and can not be planted conveniently. However, my results indicate that partial root pruning at the time of transplanting could be very beneficial in stimulating more new absorbing roots than might grow on the intact root system. The desirability of removing as much as one-half of the root system would be questionable. A number of studies have shown that although the rate of water and nutrient absorption is greatest through the unsuberized, white area of the root systems, considerable quantities of these materials can move through suberized roots as well (Kramer, 1949). The best root-pruning treatment would probably be one that provided a large number of severed lateral root tips without appreciably reducing the total length of the lateral root system.

CHAPTER VI

SHOOT AND ROOT GROWTH OF DIFFERENT SCOTCH PINE PROVENANCES AT VARYING MOISTURE-FERTILITY TREATMENTS

There has been considerable work relating differences in fertility requirements of different species of forest trees. Wilde (1938 and 1958) reported large differences in nursery soil requirements of different species. Rennie (1955) showed that forest trees generally have lower fertility requirements than do agricultural crops. Others, including those of Rennie (1955), Leyton (1957) and Ovington (1956a and 1956b), have shown that hardwood species generally have higher fertility requirements than do conifers. The studies of Mitchell and Chandler (1939) with hardwoods and of Heiberg and White (1951) with conifers also indicate considerable differences in nutrient requirements within the broad groupings of hardwoods and conifers. A number of greenhouse studies have also shown differences in optimum fertility requirements for different species, including those of Mitchell (1934) with white and Scotch pines, Fowells and Krauss (1959) with loblolly and Virginia pines, Ingsted (1957, 1959, and 1960) with birch, spruce and pines, and Sucoff (1961) with loblolly and Virginia pines.

Variations in optimum fertility levels for growth of different varieties or origins of the same species have been noted for a number of agricultural and horticultural species. Studies with peaches (Hayward <u>et al.</u>, 1946) and citrus (Haas, 1945a and 1945b; Smith, 1949; Jones, 1957) showed that variety of rootstock used in grafting caused differences in mineral nutrient requirements and growth of scions. Haas (1947) found differences in nutrient requirements of different varieties of date palm and Borden (1936) noted significant variations in growth of three varieties of sugar cane on the same soils.

There has been only a limited number of studies, however, which have been concerned with differences in nutrient requirements of different varieties, origins or clones of the same species of forest trees. Some work has been done with seed orchards and in tree improvement research programs. Studies with poplars (Mayer-Krapoll, 1952; Muller and Mayer-Krapoll, 1953) and slash pine (Goddard and Strickland, 1966) showed significant differences in the fertility requirements of different clones of the species concerned.

PROCEDURE

For this study, three origins of Scotch pine were selected: MSFG 543 from south-central Sweden; MSFG 253 from Germany; and MSFG 219 from Spain (Table 21). Earlier studies had shown that their top growth rates were very different (Wright and Bull, 1963) and that root systems of seedlings from the three areas were different in both type and extent (Chapter III). Seed was originally collected for use in the Scotch pine provenance study conducted by Wright and Bull (1963).

Seedlings were grown in the greenhouse for a period of 90 days under three levels of moisture and three levels of fertility, using a factorial design with four replications and 2-tree plots.

One-gallon glazed pots were filled with 4000 grams of a mixture consisting of 98 percent (by weight) of an inert, coarse (20 to 60 mesh) silica sand and two percent organic matter. The organic matter was added to increase the water holding capacity of the potting medium. One of three levels of a 20-10-20 fertilizer were mixed thoroughly with the potting mixture: (1) 250 milligrams to give approximately 10 ppm N, 5 ppm P_2O_5, and 10 ppm K_2O; (2) 1250 milligrams to give approximately 60 ppm N, 30 ppm P_2O_5, and 60 ppm K_2O; and (3) 2250 milligrams to give approximately 110 ppm N, 55 ppm P_2O_5 and 110 ppm K_2O. The middle level of these three approximates the optimum range reported by Wilde (1938 and 1958) for growth of Scotch pine seedlings in the nursery.

Five of the pots which had been prepared as described above were selected at random. They were saturated with water and weighed. Over

Table 21. Location and climate at place of origin of Scotch pine seed sources used in moisture-fertility study.

MSFG No., Country of Origin(a)	Lat. N.	Long. E.	Elev.	Temperature Annual	Temperature April-Sept.	Precipitation Annual	Precipitation April-Sept.	Aridity Index(b) Annual	Aridity Index(b) April-Sept
	o	o	feet	$^oC.$	$^oC.$	-millimeters-		---number----	
219 SPA	40.8	-4.0	4900	6.8	11.8	1097	464	65	21
253 GER	49.1	7.8	1300	9.5	15.0	612	338	32	14
543 SWE	60.0	12.9	625	6.2	12.6	630	350	39	15

(a) Numbers are those used in the Michigan State Forest Genetics accession record. The countries are SPAin, GERmany, and SWEden.

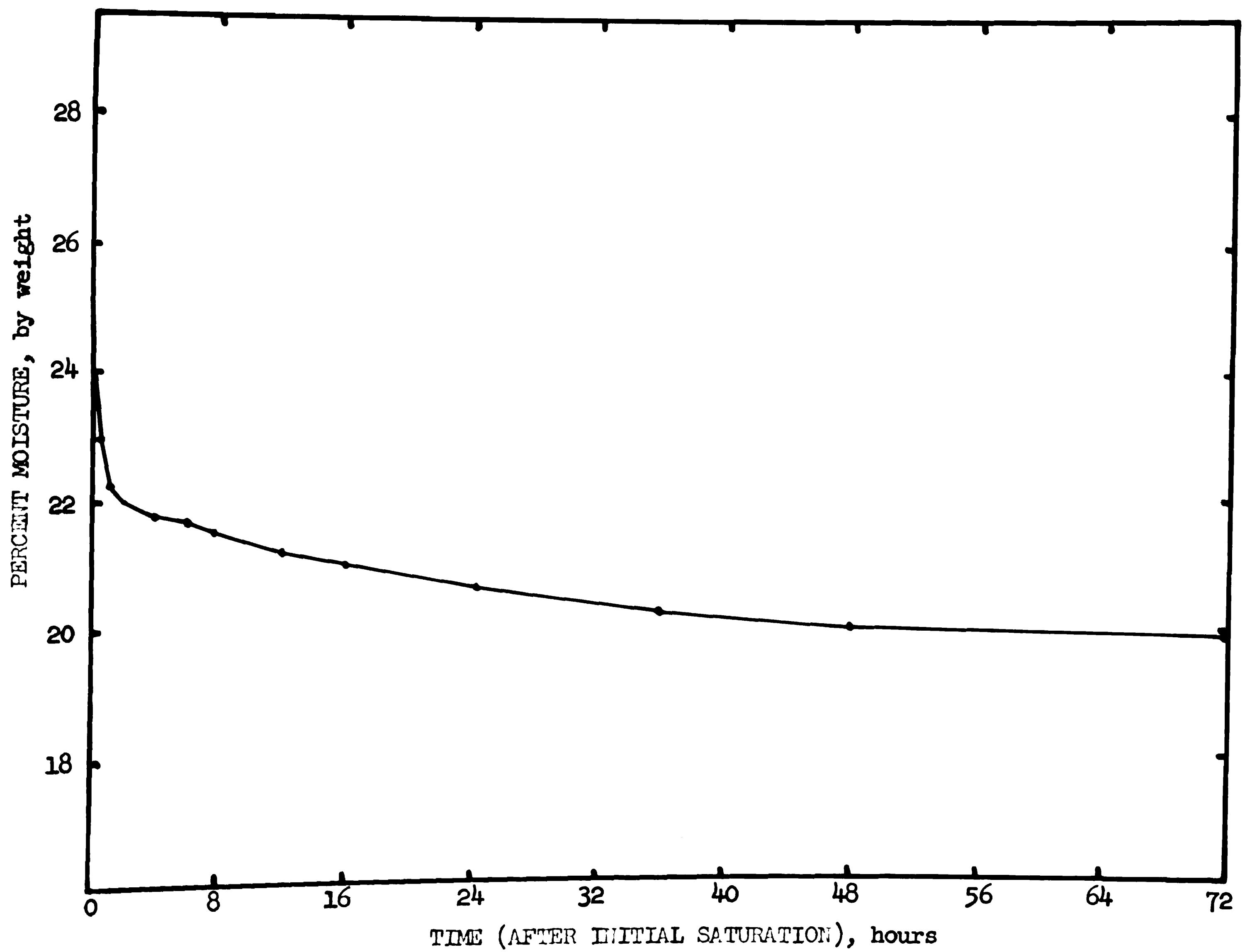
(b) Aridity Index: (DeMartonne, 1926) $\text{Index} = \frac{\text{Precipitation in mm.}}{\text{Temperature in } ^oC. + 10}$

a four-day period the pots were reweighed at intervals and percent moisture was calculated for each time of weighing. All values were plotted on a moisture depletion curve (Figure 27). Field capacity of the mixture was taken as that moisture content where the loss of water had essentially ceased and the weight of the pot and contents had become stable. The value used was 20 percent, by weight.

Pots were regulated to one of three ranges of moisture during the study: (1) between field capacity and 75 percent of field capacity; (2) between field capacity and 50 percent of field capacity; and (3) between field capacity and 25 percent of field capacity. Each individual pot was marked with the level which it was to receive and the container and dry potting mixture were weighed. The weight at field capacity was calculated and this value recorded on the side of the pot. (Weight at field capacity = weight of pot + 4000 grams + 4000 x 0.2.) The weight at the lower moisture limit was calculated and this value was also recorded on the side of the container. (For example, pots receiving the middle moisture treatment would have a lower limit of: Weight at 50 percent of field capacity = weight of pot + 4000 grams + 4000 x 0.1.) During the study moisture levels in individual pots were regulated by placing each container on a platform scale. If the weight was at or below the lower moisture limit, water was added to bring the weight up to the upper recorded level. If the weight was above the lower recorded limit, no water was added. Demineralized water was used to avoid the addition of unequal amounts of dissolved bases and other impurities present in tap water.

Seed was first sown in flats filled with the sand described

Figure 27. Moisture loss from potting mixture consisting of 98 percent (by weight) coarse, quartz sand and 2 percent organic matter.


28
26
24
22
20
18
PERCENT MOISTURE, by weight
0
8
16
24
32
40
48
56
64
72
TIME (AFTER INITIAL SATURATION), hours

previously (with no organic additive or fertilizer). One week after seed germination, seedlings were transplanted to the 108 individual pots used (3 sources x 3 moisture levels x 3 fertility levels x 4 replications), with two seedlings in each pot (two tree plots). Seedlings were grown for a 90-day period in the greenhouse, maintaining moisture at desired levels during this period. After 90 days, pots were taken from the greenhouse and the potting mixture was carefully washed from the root systems. Top and root measurements were made immediately on all seedlings (Tables 23, 24). Analyses of variance for a factorial design with 27 treatment combinations were made using means of the 2-tree plots as items (Table 22). Trend analyses were run using orthogonal polynomials and treatment sums as items.

Table 22. Analyses of variance for top and root growth of three origins of Scotch pine grown at nine moisture-fertility treatment combinations.

Source of variation	Degrees of Freedom	F ratios for								
		Top		Tap Root		Lateral Root		Tot. No.	Shoot-Root Ratio	
		Length	Weight	Length	Weight	Length	Weight	Laterals	Length	Weight
Total	107	--	--	--	--	--	--	--	--	--
Replication	4	--	--	--	--	--	--	--	--	--
Seed Source	2	188.3***	189.4***	13.8***	172.8***	54.1***	42.3***	46.8***	149.2***	29.8***
Moisture Level	2	61.5***	99.4***	151.1***	87.3***	181.3***	72.2***	125.2***	188.5***	48.4***
Fertility Level	2	26.4***	88.0***	22.7***	84.5***	44.9***	69.6***	37.6***	122.7***	6.3***
Source x Moisture	4	6.8***	48.2***	19.8***	31.3***	19.2***	12.1***	10.2***	82.7***	5.6***
Source x Fertility	4	14.2***	42.3***	28.4***	31.1***	13.9***	12.1***	6.0***	115.6***	2.8***
Moisture x Fertility	4	6.1***	20.7***	39.1***	36.2***	29.0***	40.4***	31.2***	41.0***	11.8***
Source x Moisture x Fertility	8	2.9***	8.1***	5.2***	10.6***	15.1***	17.1***	12.8***	43.2***	2.6**
Error	78	--	--	--	--	--	--	--	--	--

** Significat at 1 percent level.
*** Significant at 0.1 percent level.

RESULTS

Results showed that two of the sources, MSFG 253 and 243, reacted similarly to the moisture-fertility treatment combinations used in the study. The third source, MSFG 219, generally showed a different type and wider range of response to the different treatments. In the sections that follow, discussions are concerned primarily with differences and/or similarities between the origins used and of interactions of the seed sources with moisture and fertility levels. Main effects of fertility and moisture are not discussed for two reasons: it was not the purpose of the study to investigate variations caused by these factors, but rather to see if different origins of Scotch pine reacted similarly as these factors were varied; and because of significant differences in growth of origins at different moisture and fertility combinations, averages or main effects for these two factors would be meaningless when considered independently.

Top Growth

Top growth varied significantly due to seed source, moisture level and fertility level. All second- and third-order interactions were also significant (Tables 22, 23). It was also found that there were differences in growth patterns for top lengths as opposed to those for top weights of seedlings.

Average shoot length was greatest for seedlings of MSFG 253 and least for MSFG 543 (Table 23). Growth at different fertility levels (independent of moisture level) varied between origins. Longest shoots of German 253 and Swedish 543 occurred when seedlings were grown at the medium fertility levels. At the low and high levels shoot length was approximately the same. For Spanish 219, seedlings grown at the low fertility level had the greatest top length and shoots became shorter as fertility level increased.

When moisture treatment was considered independently of fertility level, top length was greatest for 253 and 543 when trees were grown at high and medium moisture levels and was significantly lower at the low moisture treatment. Greatest shoot length of 219 occurred at the high moisture treatment and growth decreased at successively lower moisture levels.

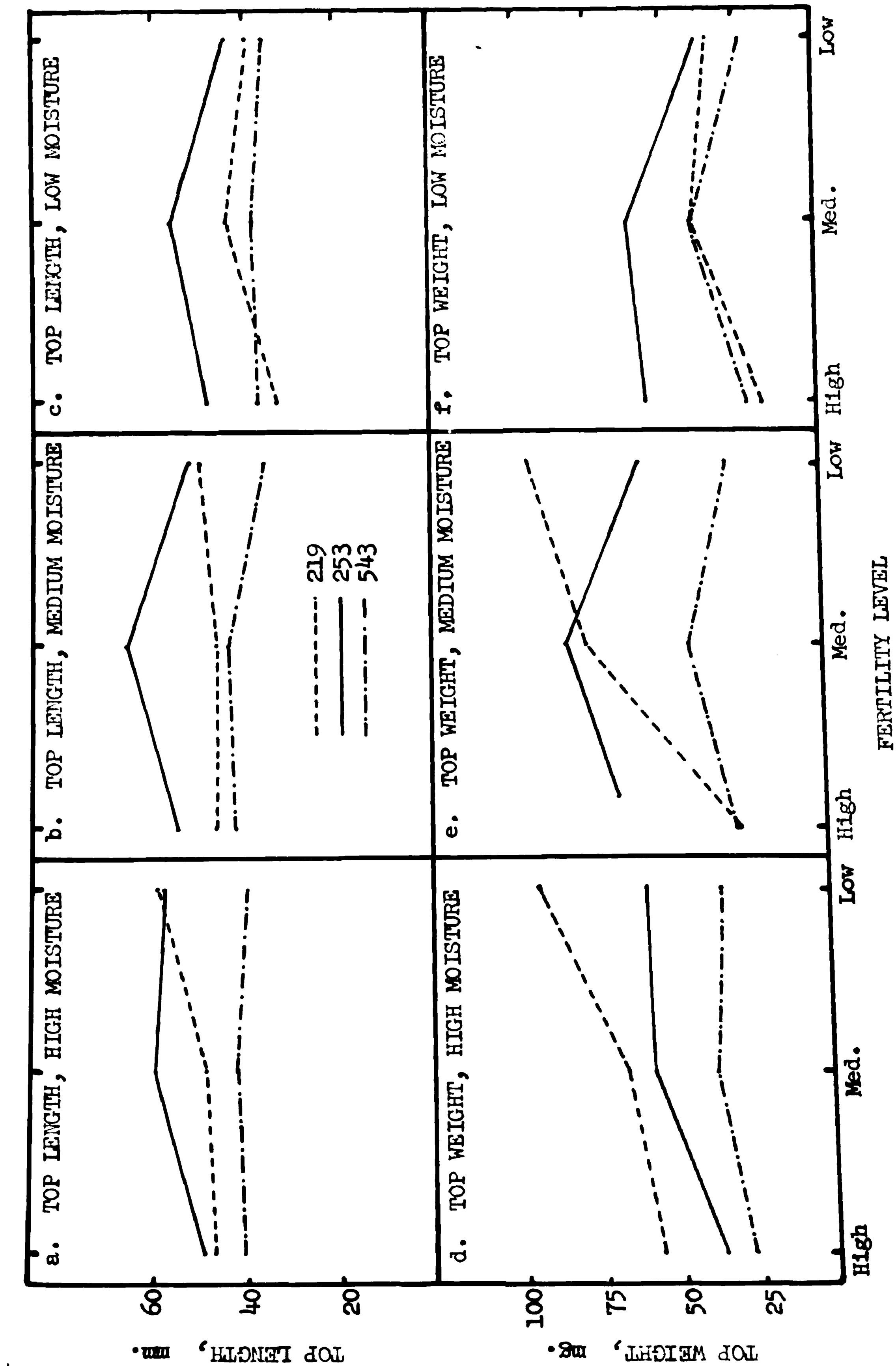
Shoot length also showed significant seed source-moisture-fertility interactions (Figure 28). MSFG 543 and 253 had their greatest top length at the medium fertility level for all three moisture levels. Growth at low and high fertility levels was approximately the same. However, top length of MSFG 219 was greatest at the low fertility level when seedlings were grown using high or medium moisture

Table 23. Top and root growth of three seed source of Scotch pine grown at different moisture-fertility treatments.

MSFG No., Country of Origin(a)	Moist. Level	Fert. Level	Top Length	Top Weight	Tap Root Length	Tap Root Weight	Lateral Root Length	Lateral Root Weight
			mm.	mg.	mm.	mg.	mm.	mg.
219 SPA	High	High	48	57	180	10	612	11
		Med.	50	67	181	10	553	11
		Low	59	95	291	19	1048	21
	Med.	High	48	28	86	6	25	1
		Med.	48	78	189	14	562	13
		Low	53	97	207	14	749	18
	Low	High	34	18	32	4	6	1
		Med.	46	41	156	9	246	3
		Low	40	35	73	6	38	3
Averages for MSFG 219			47	57	155	10	427	10
253 GER	High	High	50	37	174	5	494	7
		Med.	60	58	176	8	878	14
		Low	58	60	257	9	1146	20
	Med.	High	55	68	182	6	581	11
		Med.	66	84	188	8	594	11
		Low	54	60	158	6	341	6
	Low	High	49	57	136	6	357	9
		Med.	57	62	140	6	558	13
		Low	45	39	97	5	71	4
Averages for MSFG 253			55	59	168	6	558	11
543 SWE	High	High	41	28	156	6	263	5
		Med.	43	38	146	7	481	10
		Low	41	36	177	8	552	13
	Med.	High	43	29	149	5	263	5
		Med.	45	45	156	7	332	7
		Low	37	31	123	6	182	4
	Low	High	38	23	142	5	166	3
		Med.	39	41	153	7	415	9
		Low	37	24	91	5	182	3
Averages for MSFG 543			40	33	143	8	433	9
LSD's, .05 level for:								
1. Main Effects			1.5	3.0	9.2	.5	46.7	.9
2. 1st Order Int.			2.7	5.1	15.8	.8	80.3	1.6
3. 2nd Order Int.			4.6	8.9	27.4	1.4	137.6	2.7

(a) SPAin, GERmany, SWEden.

Figure 28. Top growth of three seed sources of Scotch pine at nine moisture-fertility treatment combinations.


a. TOP LENGTH, HIGH MOISTURE
b. TOP LENGTH, MEDIUM MOISTURE
c. TOP LENGTH, LOW MOISTURE
d. TOP WEIGHT, HIGH MOISTURE
e. TOP WEIGHT, MEDIUM MOISTURE
f. TOP WEIGHT, LOW MOISTURE
219
253
543
TOP LENGTH, mm.
60
40
20
TOP WEIGHT, mg.
100
75
50
25
High
Med.
Low
FERTILITY LEVEL

treatments and at the medium fertility level when they were grown at low moisture.

For the nine moisture-fertility treatments, maximum shoot lengths occurred at the medium moisture-medium fertility combination for seedlings of German 253 and Swedish 543 and at the high moisture-low fertility combination for Spanish 219 (Figure 28).

Weights of seedling shoots showed some decided differences from the patterns described for top lengths. Average top weights were approximately equal for MSFG 219 and 253 and were significantly lower for MSFG 543 (Table 23). There were significant differences, however, when seedlings were grown at different moisture and fertility combinations. At high moisture levels (independent of fertility level) top weights were greatest for MSFG 219. At the medium moisture treatment, weights were approximately the same for 253 and 219 and significantly lower for 543. At the low moisture treatment, seedlings of 253 were heaviest, while those for 219 and 543 were about the same. Similar patterns were noted when fertility level was considered independent of moisture level. Highest shoot weights of 253 and 543 occurred when seedlings were grown at medium fertility levels and heaviest shoots for 219 when seedlings were grown at the low fertility level.

Heaviest shoot weights for the nine moisture-fertility treatments were recorded when 253 and 543 were grown at the medium moisture-medium fertility treatment. The maximum for 219 was found when seedlings were grown at the high moisture-low fertility combination (Figure 28).

Because of differences in patterns for top lengths and top weights, there were prounounced differences in the weight per unit length of seedling shoots. For MSFG 253 and 543 values were approximately equal and varied only slightly at different moisture and fertility levels. Average weight per unit length was generally greatest for seedlings of MSFG 219. It was found, however, that weight per unit length of shoots of this source increased as moisture level increased and decreased as fertility level became higher.

Trend analyses (using orthogonal polynomials) showed that the nature of the relationships between seed sources and varying moisture-fertility combinations were not the same. Trends (lengths and weights) for Swedish 543 and German 253 were generally curvilinear in relation to increasing or decreasing fertility levels. At high and medium moisture treatments these trends were strongly curvilinear, while at the low moisture level it was slightly curvilinear. Trends for 219 were linear at high and medium moisture levels in relation to varying fertility treatments. At the low moisture level, trends for 219 varied from slightly curved for shoot weight to curved for shoot length.

The major cause of trend differences for Spanish 219 as opposed to those for German 253 and Swedish 543 was restricted growth of seedlings of the Spanish source at high fertility levels, particularly in combination with low and medium moisture levels.

Root Growth

Root growth showed significant differences depending upon the particular combination of moisture and fertility at which seedlings of the three origins were grown (Table 23). Seedlings of MSFG 543 had the smallest average root systems in terms of laterals and tap roots, lengths and weights. Average lengths of laterals and taproots were greatest for MSFG 253. However, as was noted with seedling tops, weight per unit length was generally greater for roots of Spanish 219. This was particularly true of the tap roots. At many moisture-fertility combinations roots of 219 were heavier than those of 253 and 543 (Figures 29, 30). As a result, there were no significant differences in average lateral root weights for MSFG 253 and 219 and the tap roots of 219 were significantly heavier than those of the other two origins. This high weight per unit length of roots of Spanish origins of Scotch pine is a character noted in Chapter III.

There were a number of major differences between the patterns for root growth and those for top growth. When moisture treatment was considered independently of fertility level, length and weight of lateral and tap roots of all sources were greatest at the high moisture level. This was contrasted to top growth where maximum growth of 253 and 543 occurred when seedlings were grown at the medium moisture level.

There were also differences when fertility level was considered independently of moisture level. MSFG 219 showed greatest lengths and weights of tap and lateral roots at the low fertility level and growth decreased as fertility level increased. Growth of roots of

Figure 29. Tap root growth of three seed sources of Scotch pine at nine moisture-fertility treatment combinations.

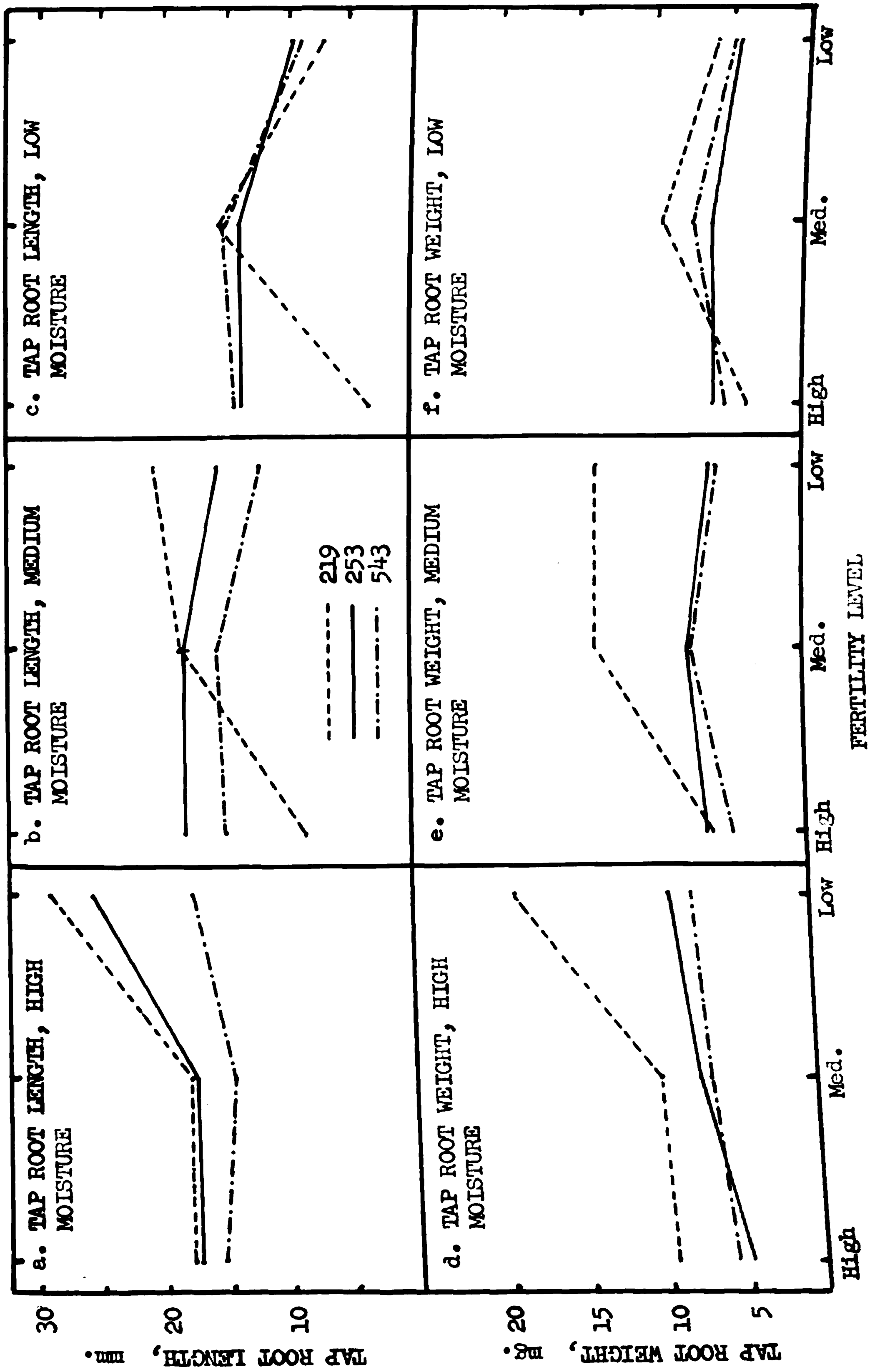
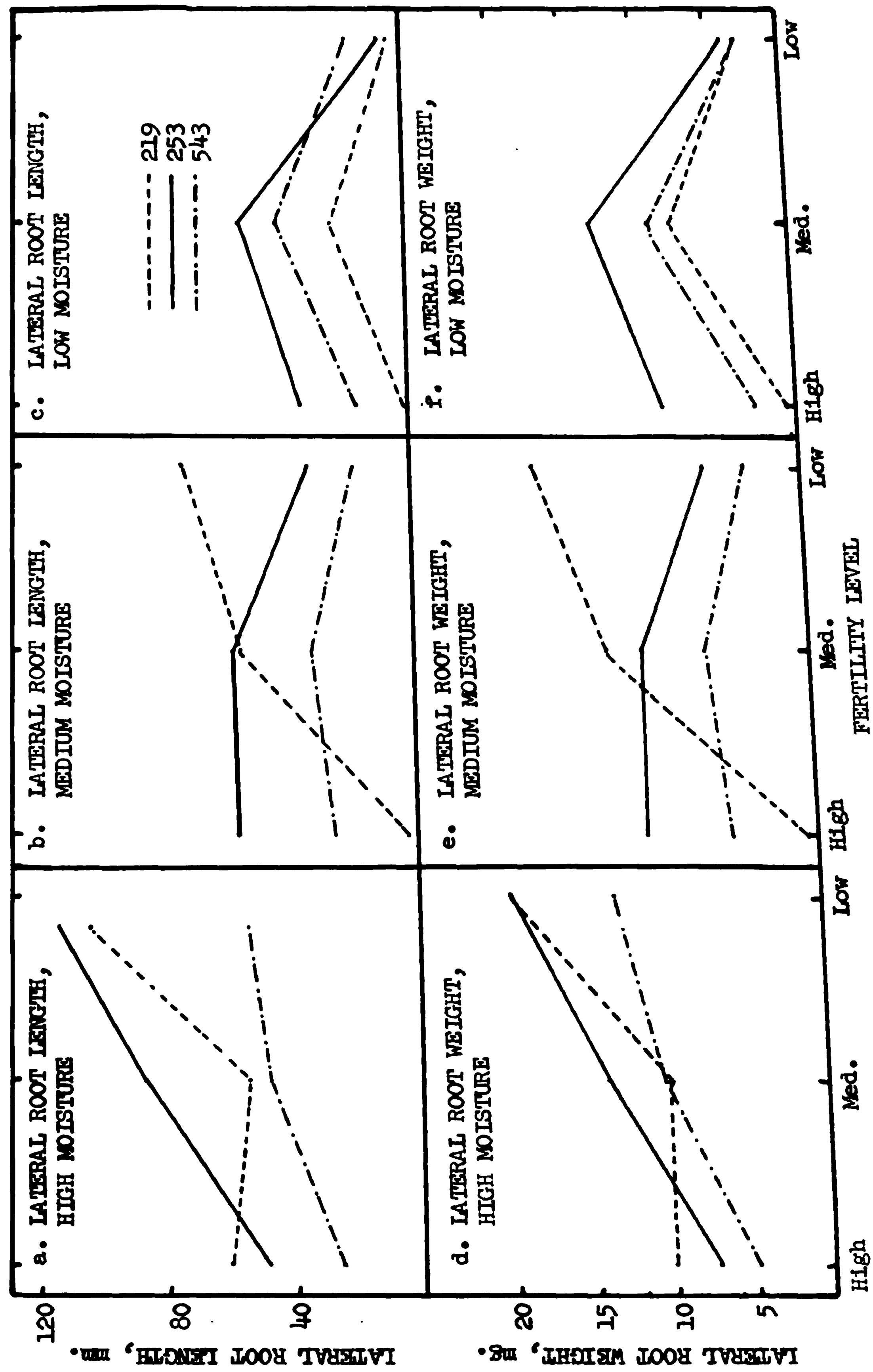

a. TAP ROOT LENGTH, HIGH MOISTURE
b. TAP ROOT LENGTH, MEDIUM MOISTURE
c. TAP ROOT LENGTH, LOW MOISTURE
d. TAP ROOT WEIGHT, HIGH MOISTURE
e. TAP ROOT WEIGHT, MEDIUM MOISTURE
f. TAP ROOT WEIGHT, LOW MOISTURE
219
253
543
TAP ROOT LENGTH, mm.
30
20
10
TAP ROOT WEIGHT, mg.
20
15
10
5
High
Med.
Low
FERTILITY LEVEL

Figure 30. Lateral root growth of three seed sources of Scotch pine at nine moisture-fertility treatment combinations.


a. LATERAL ROOT LENGTH, HIGH MOISTURE
b. LATERAL ROOT LENGTH, MEDIUM MOISTURE
c. LATERAL ROOT LENGTH, LOW MOISTURE
219
253
543
d. LATERAL ROOT WEIGHT, HIGH MOISTURE
e. LATERAL ROOT WEIGHT, MEDIUM MOISTURE
f. LATERAL ROOT WEIGHT, LOW MOISTURE
LATERAL ROOT LENGTH, mm.
120
80
40
LATERAL ROOT WEIGHT, mg.
20
15
10
5
High
Med.
Low
FERTILITY LEVEL

219 was very restricted at the high fertility level (Table 23). Fertilizer salt concentration appeared to be near the toxic level when seedlings of 219 were grown at the high fertility level in combination with low moisture (Figure 31). Growth of the root systems of MSFG 543 and 253, on the other hand, was greatest at the medium fertility level. Although growth of these two origins was least at the high fertility level, it was not so restricted as was that of MSFG 219 (Figures 32, 33).

Tap and lateral root lengths and weights were maximum at the same moisture-fertility combination for all three seed sources -- that of high moisture and low fertility (Figures 29, 30). This was opposed to top growth where lengths and weights of MSFG 253 and 543 were greatest at the medium moisture-medium fertility treatment. This same phenomenon of lower fertility levels for maximum root growth than those for best shoot growth has been recorded in a number of other studies, including those of Demortier and Fourage (1938) with Scotch pine, Mitchell (1939) with white pine, Bensend (1943) with jack pine, and Fowells and Krauss (1959) with Virginia pine.

There were also differences in development for seedlings grown at different moisture-fertility combinations. All sources showed significant linear trends in relation to varying fertility levels at the high moisture treatment, with greatest root lengths and weights at the low fertility level. At medium and low moisture levels, root growth was similar to that for shoot growth. MSFG 253 and 543 had greatest root weights and lengths at medium fertility levels. Trends in relation to varying fertility levels were curvilinear. At the medium moisture treatment, root growth of 219 was

Figure 31. Growth of Spanish MSFG 219 at two moisture-fertility combinations: low moisture-high fertility (left) and high moisture-low fertility (right).

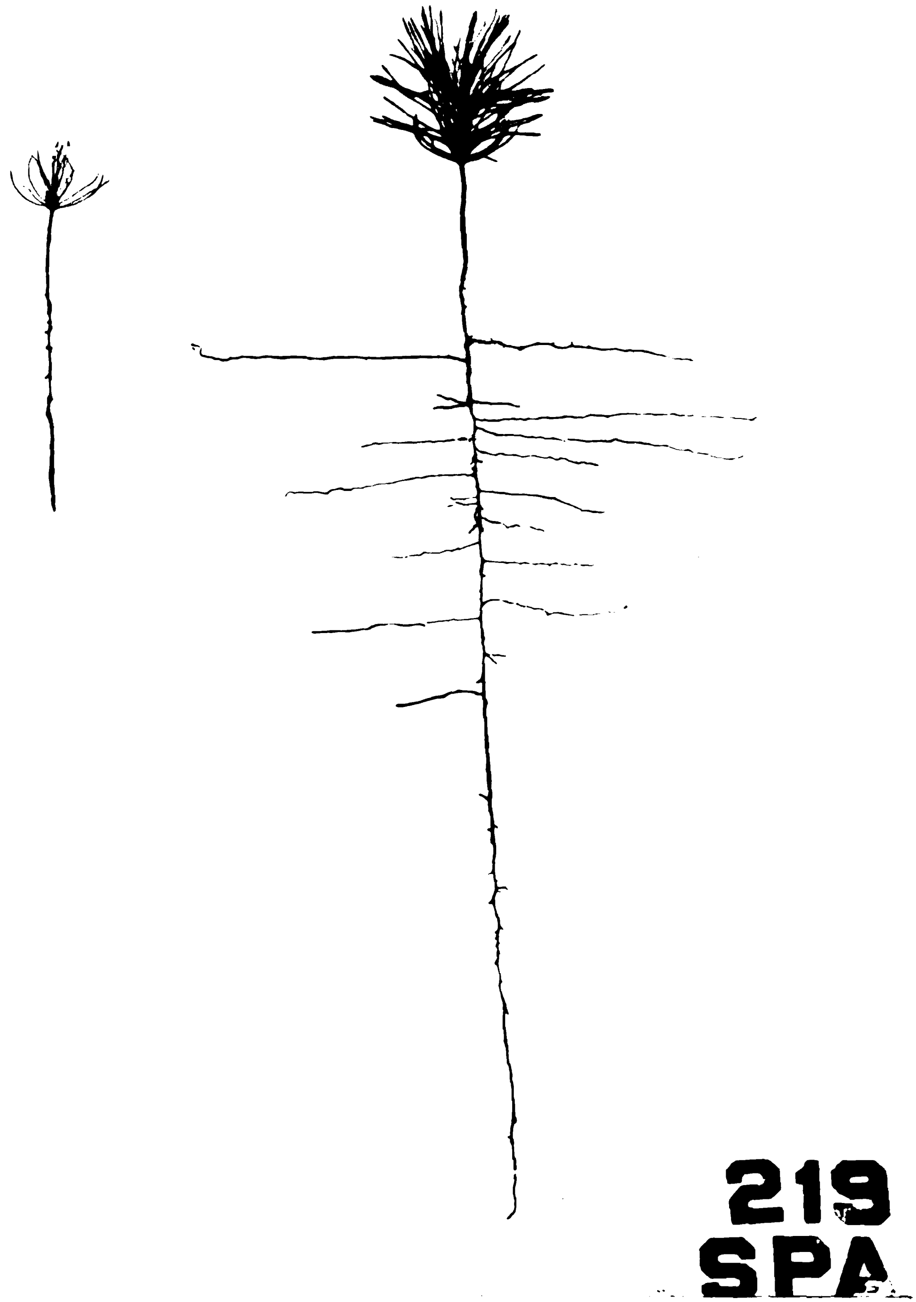


Figure 32. Growth of German MSFG 253 at two moisture-fertility combinations: low moisture-high fertility (left) and high moisture-low fertility (right).

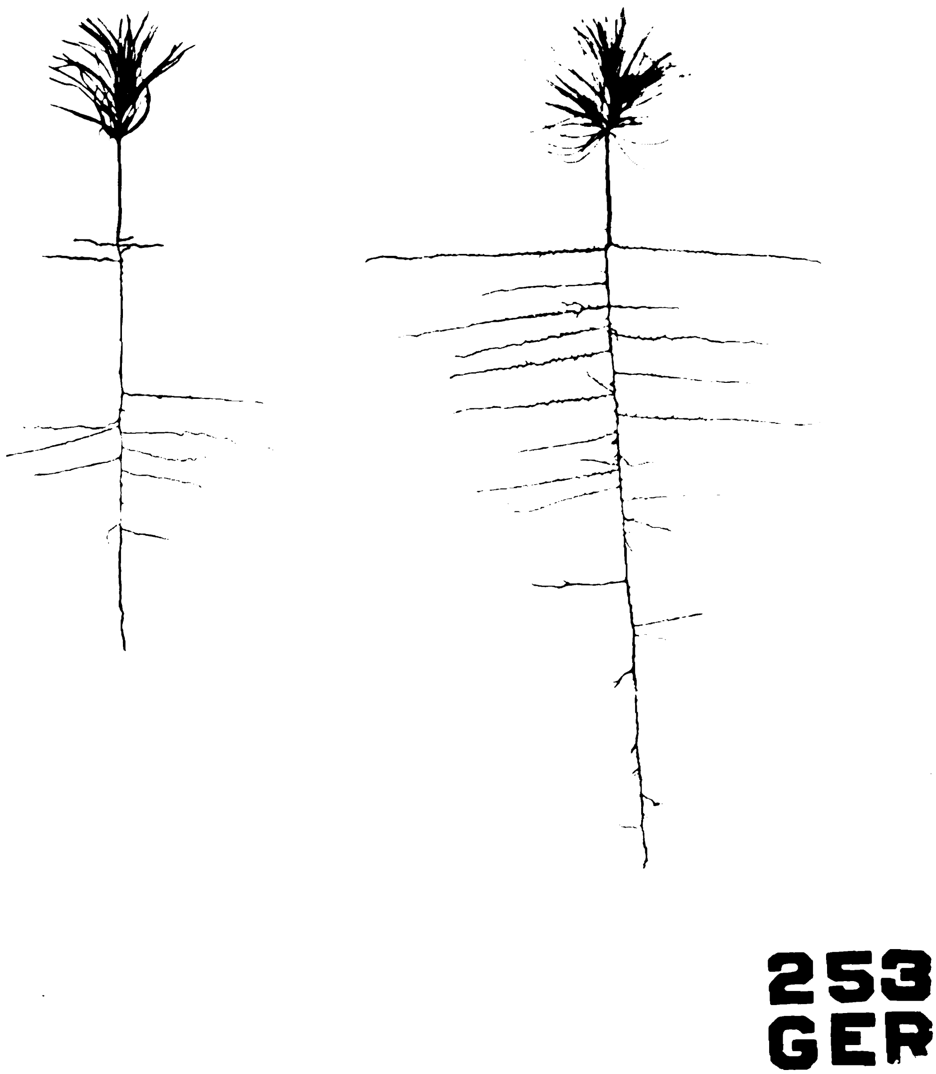
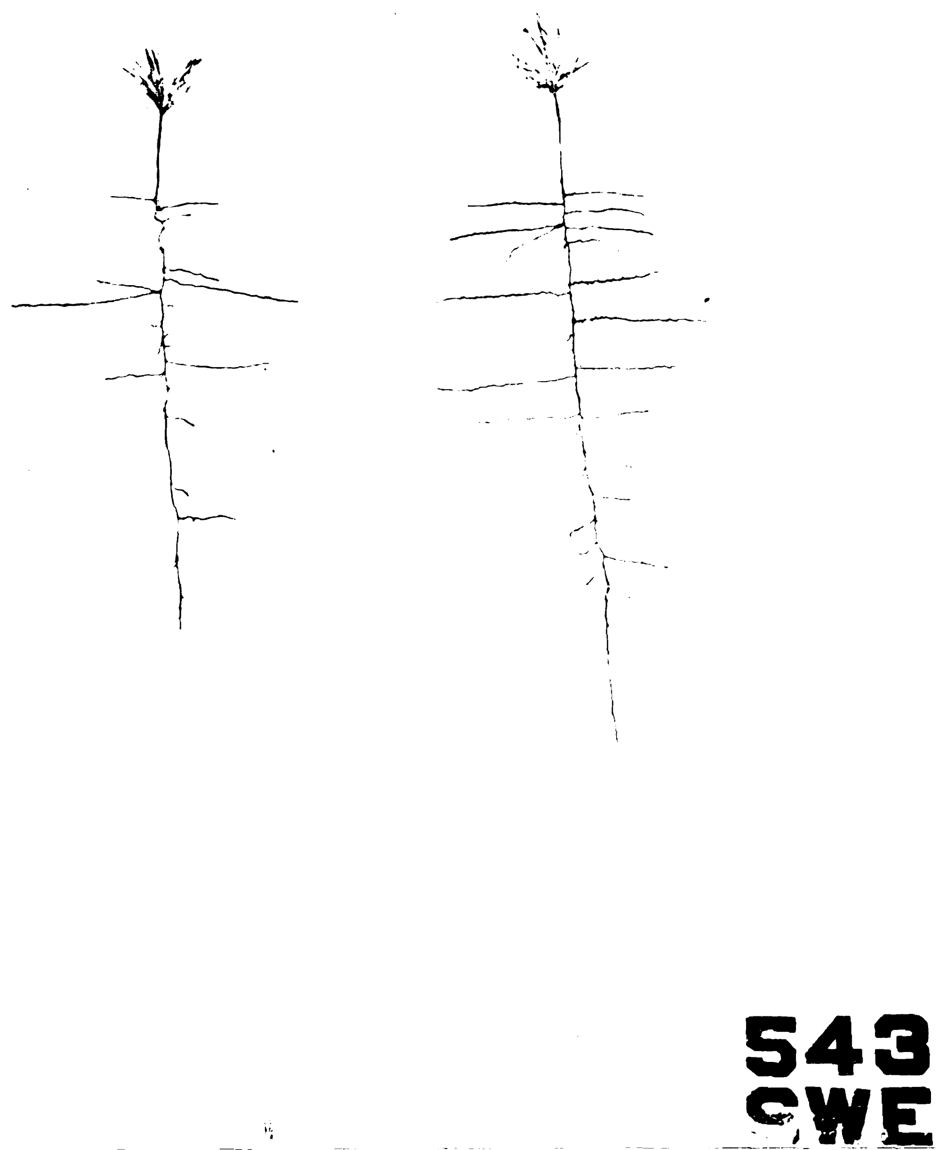


Figure 33. Growth of Swedish MSFG 543 at two moisture-fertility combinations: low moisture-high fertility (left) and high moisture-low fertility (right).



greatest at the low fertility level, with a linear trend in relation to differing fertility levels. At the low moisture treatment, growth of roots of 219 was greatest at the medium fertility level and the trend was curvilinear.

The total number of lateral roots which formed and the degree of branching was generally closely correlated ($r = 0.94$) with lateral root length. There were differences associated with seed source and treatment, however. The root systems of MSFG 219 were approximately 30 percent less branched than those of MSFG 253 and 543. MSFG 253 had the greatest amount of branching and this source had the highest number and greatest percentage of lateral roots which were branched twice (Table 24). This character of low branching of Spanish origins of Scotch pine has been noted in Chapter III.

Different moisture and fertility treatments also affected the number of lateral roots and degree of branching of the root systems. In general, the greatest number of laterals and highest degree of branching occurred on seedlings grown at high moisture levels and decreased as moisture level decreased. The reverse occurred with changes in fertility level. Maximum numbers and branching were found on trees grown at low fertility levels and numbers and branching decreased as fertility became higher. These patterns varied somewhat with seed source. The greatest number of laterals for MSFG 253 and 219 occurred on trees grown at the high moisture-low fertility combination. For MSFG 543 maximum numbers were found on seedlings grown at the high moisture-medium fertility combination.

Table 24. Lateral roots per tree, proportion of branched lateral roots and shoot-root ratios of three origins of Scotch pine grown at different moisture-fertility treatments.

MSFG No., Country of Origin(a)	Moist. Level	Fert. Level	Total Lateral Roots /tree	Proportion of total lateral roots with number of branches 0	1	2	Shoot-Root Ratio Shoot Wt. / Tot. Rt. Wt.	Shoot L. / Tot. Root Length
			number	-----percent-----			-------ratio-------	
219 SPA	High	High	121	78	22	0	2.84	.063
		Med.	118	80	19	1	3.20	.072
		Low	254	80	19	1	2.41	.046
	Med.	High	24	100	0	0	4.21	.435
		Med.	122	74	25	1	2.92	.064
		Low	178	77	23	Trace	3.19	.056
	Low	High	4	100	0	0	4.30	.910
		Med.	83	81	19	0	2.43	.114
		Low	16	93	7	0	3.93	.351
Averages for MSFG 219			102	79	21	Trace	3.27	.234
253 GER	High	High	130	78	22	0	3.10	.077
		Med.	223	80	19	1	2.70	.058
		Low	401	84	15	1	2.08	.042
	Med.	High	165	74	23	3	3.95	.072
		Med.	167	76	22	2	4.63	.087
		Low	119	72	28	0	4.83	.109
	Low	High	84	71	29	0	3.87	.099
		Med.	150	78	21	1	3.22	.083
		Low	35	69	30	1	4.66	.267
Averages for MSFG 253			164	78	21	1	3.67	.099
543 SWE	High	High	77	70	30	0	2.60	.099
		Med.	192	86	13	1	2.25	.068
		Low	153	79	20	1	1.72	.059
	Med.	High	80	74	26	0	2.91	.104
		Med.	34	83	17	Trace	3.17	.092
		Low	73	76	24	0	3.43	.124
	Low	High	79	81	19	0	3.00	.122
		Med.	104	73	26	1	2.47	.073
		Low	63	72	28	0	3.14	.133
Averages for MSFG 543			100	78	22	Trace	2.74	.097
LSD's, .05 level for:								
1. Main Effects			15	--	--	--	.25	.018
2. 1st Order Int.			26	--	--	--	.42	.032
3. 2nd Order Int.			44	--	--	--	.72	.054

(a) SPAin, GERmany, SWEden.

Shoot-Root Ratios

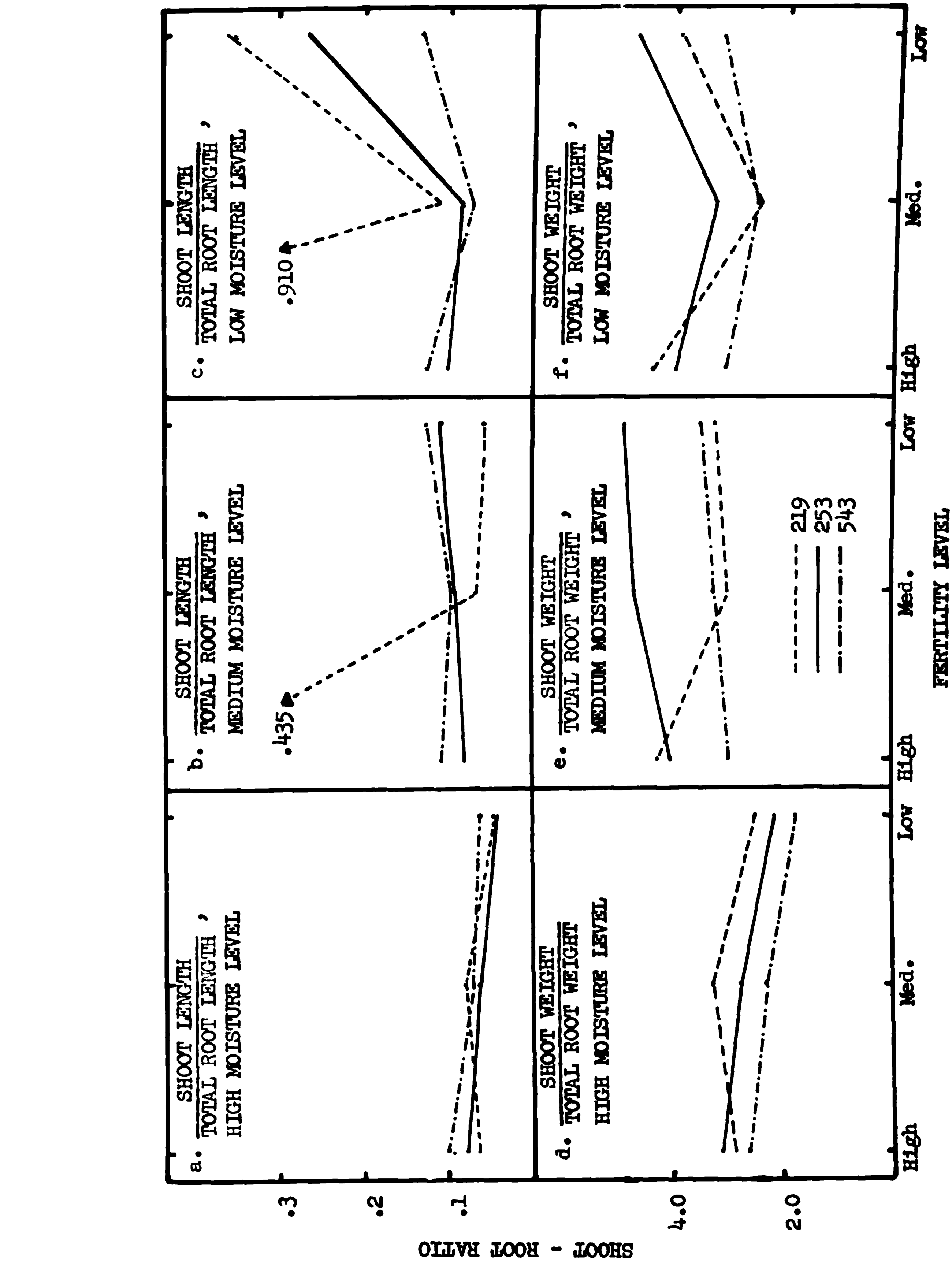
Shoot-root ratios are most commonly calculated using weights of seedling tops and root systems. Such ratios are more easily determined than those requiring measurement of the length of root systems. For seedlings grown in this study, there were decided differences in shoot-root ratios obtained using weights and those calculated using lengths. These were primarily differences in averages for the three origins and in ranking of ratios for the sources at different moisture-fertility combinations (Table 24, Figure 34).

Average shoot-root ratios calculated using seedling weights were significantly highest (most unfavorable) for MSFG 253 and were lowest for MSFG 543. However, when ratios were determined using seedling lengths, averages were approximately the same for 253 and 543 and were highest for 219. These differences were caused by variations in weight per unit length of seedling tops and root systems and by severe restriction of growth of MSFG 219 at some moisture-fertility combinations.

There were significant seed source-moisture, seed-source fertility and seed source-moisture-fertility interactions (Table 22). Ratios for 253 and 543 (independent of moisture treatment) were approximately the same when seedlings were grown at all fertility levels. For MSFG 219, however, ratios were most favorable at low to medium fertility levels and significantly highest at the high fertility treatment. At different moisture treatments (independent of fertility levels), ratios for all sources were best at the high moisture level.

Lowest shoot-root ratios (based on lengths and weights) occurred

Figure 34. Shoot-root ratios of three seed sources of Scotch pine grown at nine moisture-fertility treatment combinations.


SHOOT - ROOT RATIO
.3
.2
.1
4.0
2.0
a. SHOOT LENGTH / TOTAL ROOT LENGTH , HIGH MOISTURE LEVEL
b. SHOOT LENGTH / TOTAL ROOT LENGTH , MEDIUM MOISTURE LEVEL
c. SHOOT LENGTH / TOTAL ROOT LENGTH , LOW MOISTURE LEVEL
d. SHOOT WEIGHT / TOTAL ROOT WEIGHT HIGH MOISTURE LEVEL
e. SHOOT WEIGHT / TOTAL ROOT WEIGHT , MEDIUM MOISTURE LEVEL
f. SHOOT WEIGHT / TOTAL ROOT WEIGHT , LOW MOISTURE LEVEL
.435
.910
219
253
543
High
Med.
Low
FERTILITY LEVEL

for all origins with seedlings grown at the high moisture-low fertility combination. This was the treatment at which root weights and lengths were greatest for all sources. It was also the treatment at which top growth of 219 was generally highest (Figures 27, 28, 29).

At other moisture-fertility combinations, there were a number of differences between origins. These were primarily variations between ratios for seedlings of Spanish 219 as opposed to those for German 253 and Swedish 543. At high moisture levels, shoot-root ratios for all origins were lowest when seedlings were grown at low fertility levels. When the medium moisture level was used they were minimum for 253 and 543 at the high fertility levels and for 219 at the low fertility level. At the low moisture treatment, ratios for all sources were minimum at the medium fertility level (Figure 34).

Trend analyses indicated that MSFG 253 and 543 exhibited linear relationships to varying fertility levels when grown at high and medium moisture treatments. Trends for MSFG 219 were slightly to strongly curvilinear at these moisture levels. At the low moisture treatment, trends for all sources were strongly curvilinear in relation to varying fertility levels.

Relation of Moisture and Fertility Requirements to Climate, Soils and Evolutionary History of Area of Origin

In the previous sections it was shown that two origins of Scotch pine, German 253 and Swedish 543, reacted similarly to the nine moisture-fertility treatments used in the study. The third source, Spanish 219, reacted quite differently and generally had lower fertility and higher moisture requirements than did 543 and 253.

It was impossible to determine from the information available exactly why fertility requirements for MSFG 219 might be lower than those of MSFG 253 and 543. Exact soils information was not taken when the seed was collected in Europe. However, the Instituto Forestal, the agency which collected the seed of MSFG 219, stated that collections had been made in the Sierra de Guadarrama, Spain from a relatively small stand growing on siliceous, sandy soils that had originated from granitic parent material. It was also stated that the area had been under forest management for more than 150 years.

Positive conclusions regarding the fertility of this particular soil from such scant information would be impossible. However, soils of such origin have often been found to be of low fertility status (Wilde, 1958; Lutz, 1958). Evolution on such soils could produce a species or origin in which individuals of low fertility requirement would have an adaptive advantage. Over a long period of time individuals of higher requirement might well be eliminated from the population.

This probability is strengthened when the evolutionary history of the Spanish origins of Scotch pine is considered. The range in

Spain is restricted to isolated stands at higher elevations and there is little exchange of genetic material between areas. Wright and Bull (1963) postulated that inbreeding had acted in the isolated Spanish populations, leading to genetic drift and gene fixation. Spain was well below the ice cap during Pleistocene glaciation and these processes have continued more or less uninterrupted for a longer period of time than in most areas of northern and central Europe.

Forest management could also be a factor in eliminating certain genotypes from the stand in which seed of MSFG 219 was collected. In management of species such as Scotch pine which are intolerant of reduced light intensities it is common to thin out smaller or slower growing trees from stands in favor of continued rapid growth on larger dominants and codominants. If evolution had produced an origin having low fertility requirements, continued thinning over the past 150 years would tend to remove trees of slower growth and higher fertility requirement.

No soils or geologic information was available for MSFG 543 and 253. However, seed collections were made in areas having evolutionary histories considerably different from that of MSFG 219. The modern Scotch pine populations in northern and mid-European areas probably evolved from remnant stands which survived Pleistocene glaciation in the Scandinavian highlands or to the south of the ice cap, probably in the Alps or Carpathians (Wright and Bull, 1963). After the retreat of the ice cap, the species reinvaded the glaciated areas and eventually formed extensive and often continuous forested areas. There would have been a free and constant interchange of genes between neighboring populations. Genetic drift and gene fixation would probably have been very low or entirely absent. As a result, these origins could well display intermediacy in a number of characters, including fertility requirement.

It also appeared that there were differences between origins in moisture requirements. Seedlings of MSFG 219 showed a tendency toward better growth at higher moisture levels than those required by MSFG 543 and 253. The annual precipitation of the area from which 219 was collected was over 1000 millimeters, while that for the areas from which MSFG 543 and 253 were collected was 630 and 612 millimeters, respectively. Precipitation for the growing season was 464 millimeters for MSFG 219, 338 millimeters for MSFG 253 and 350 millimeters for MSFG 543 (Table 21). For the whole year, Aridity Index values (which are measures of effective precipitation) for the three areas were 65 for MSFG 219, 39 for MSFG 543 and 32 for MSFG 253. For the growing season months, the values were 21, 15, and 14, respectively, for MSFG 219, 543 and 253. It would appear, therefore, that the Spanish origin evolved under conditions which were considerably more moist than those of the German and Swedish origins. As a consequence it would be entirely possible for MSFG 219 to have higher moisture requirements than 543 and 253.

The time periods and evolutionary histories discussed previously would also be pertinent to differences in moisture requirements. The long evolutionary history, with isolation and inbreeding, could favor gene fixation and high moisture requirement in the Spanish population. In the Swedish and German areas, shorter evolutionary histories and ready exchange of genetic material could have favored intermediacy in moisture requirements.

CHAPTER VII

SUMMARY

Root types, patterns of root growth and growth after different cultural treatments were studied for greenhouse and nursery grown seedlings of different Scotch pine provenances. Significant differences were noted in a number of characteristics. In many instances it was possible to relate these variations to climatic conditions and past evolutionary history of the areas from which seed had been collected in Europe and Asia.

Analyses were made of root systems of 45 origins of Scotch pine which had been grown in the greenhouse for periods of four and eight months. These provenances, from throughout the species range, showed significant differences in tap root development, extent and character of lateral root growth and degree of branching of the lateral roots. Sources from northern portions of the range (including provenances of vars. mongolica, lapponica, septentrionalis, rigensis and altaica) had pronounced tap root development, with lateral root extension generally restricted to branching from the upper portions of the tap root. Length of tap roots and lateral roots was closely correlated with average annual temperature of the area of seed collection but was not correlated with precipitation.

Central European origins of vars. polonica, hercynica, haguenensis and illyrica had more moderate expression of the tap root characteristic. Lateral roots were more extensive and occurred along most of the tap root. Sources of these varieties were also more branched than those of origins from other portions of the species range. Other studies have shown that origins of these varieties are generally the fastest growing of all Scotch pine provenances. It seems probable that the fast top growth rates are associated with the extensive lateral lengths and high branching of roots. This would allow seedlings to occupy the soil very completely and to make maximum utilization of soil moisture and nutrients. Root types of central European origins could not be correlated closely with climate, possibly because of free interchange of genes in the more or less continuous populations.

The southern provenances (including origins of vars. aquitana, iberica, rhodopaea, and armena) came from isolated portions of the range and exchange of genetic material between areas was probably very limited. As a result there were a number of differences between origins from different areas. In general all southern varieties were distinctly tap-rooted. This was expressed in general appearance and high weight per unit length of roots. Lateral roots were also less branched on southern provenances than on origins from farther north. There were a number of differences, however, in lateral roots of southern provenances. Lateral rooting of south French origins (var. aquitana) was similar to that of northern varieties, with laterals extending primarily from upper portions of the tap root. This may be a reflection of colder weather conditions which prevailed during Pleistocene glaciation. Root types may have persisted because of the relative isolation of the area from other portions of the range. Spanish origins (var. iberica) had significantly longer tap roots than did all other origins. Lateral roots were short but numerous and extended from along most of the tap root. This gave the root systems of Spanish origins a narrow, columnar appearance. These were considered to be adaptive characters related to low total and growing season precipitation in the areas of seed collection. Greek provenances (var. rhodopaea) originated from moist areas and had lateral root characters which were intermediate between those of other southern varieties and those from central Europe. Turkish and Georgian SSR origins (var. armena) were deeply tap-rooted and lateral rooting was extensive. Individual laterals were not so short as those of Spanish origins, however.

Through periodic sampling of greenhouse-grown seedlings, patterns of root elongation of eight provenances were studied for the first 80 days after seed germination. Variations were shown to be related to climates of the areas from which seed had been collected.

There was an apparent interplay between tap and lateral root growth of all sources. Initial root growth was confined to tap root extension. No laterals appeared until 10 days after germination and there was no appreciable amount of lateral growth until after tap root growth began to decline 30 to 40 days after germination. After this lateral root lengths increased rapidly.

Percentage rates of tap and lateral root growth were fastest for northern origins and slowest for southern provenances from moist climates. Throughout the study period actual tap root lengths and weights were greatest for the Spanish origin used. It was postulated that the rapid percentage rates of growth of the northern provenances was related to the shortened growing seasons in the areas of seed collection. This would allow seedlings to make maximum use of the limited period during which temperatures would be most favorable for growth.

Rapid and deep penetration of tap roots of the Spanish source were probably adaptive characters related to the relatively warm, dry conditions in the area from which seed was collected.

Root growth of central European sources and southern origins from moist climates could not be correlated with temperature or precipitation. This could be related to the fact that climate is not particularly limiting for the growth of Scotch pine in those areas.

Nursery grown seedlings of five provenances of Scotch pine were transplanted at monthly intervals for the first five months after seed germination. Three intensities of root pruning were used at the time of transplanting. There were significant differences in top growth, survival, root growth and the ability of seedlings to regenerate new root systems.

A definite inverse periodicity in root and top growth was noted for all origins. During the period when top growth was most active, root elongation and root regeneration were relatively slight. It was not until after terminal shoot growth began to slow down or was completed that the majority of root growth or root regeneration took place.

Survival was closely correlated with the amount of roots present at transplanting and the growth of new roots after transplanting. During the early part of the growing season root-shoot ratios were low and neither the amount of roots present at transplanting nor new growth after transplanting was sufficient to supply moisture for the actively growing trees. Survival was very low. After the major increase in root growth which took place after height growth was completed, survival increased markedly.

Variations in seasonal patterns of survival and root growth were closely correlated with the origins used. After earlier transplantings survival was somewhat better for the two northern (Swedish) provenances. These sources were also found to have the most rapid initial rates of root growth and root regeneration.

Intensity of root pruning was found to affect survival and root regeneration after transplanting. It was significantly lower for trees which had received full root pruning than for those which had received no or half root pruning. No significant differences in average or periodic survival were noted between seedlings receiving no or half root pruning. However, seedlings which had been half root pruned produced significantly greater amounts of new root growth after transplanting than did trees which had not been root pruned.

Provenances from Spain, Germany and Sweden were grown from seed for a 90-day period in the greenhouse using nine moisture-fertility treatment combinations (3 moisture x 3 fertility). Significant differences were noted between sources in fertility and moisture requirements and in optimums for shoot and root growth. Growth of the Swedish and German sources was very similar in relation to varying moisture and fertility levels, although the actual amounts of growth were significantly different. The Spanish source reacted quite differently and generally had lower fertility requirements than did the German and Swedish origins.

Top growth was greatest for the Swedish and German origins at the medium moisture and fertility levels and was least at low moisture and low fertility treatments. Top growth of the Spanish source appeared to be closely related to fertilizer salt concentration in the soil solution. It was greatest at treatments where concentration was lowest (high moisture-low fertility) and poorest when salt concentration was maximum (low moisture-high fertility).

Optimum fertility levels for best root growth appeared to be lower than those for best shoot growth. Root lengths and weights were greatest at the same treatment combination for all sources -- that of high moisture and low fertility. At other treatments, however, there were significant differences between sources in root growth. These differences indicated that, in general, fertility levels for best root growth were somewhat lower for the Spanish provenance than for the Swedish and German origins.

Weight per unit length of shoots and roots of the Spanish origin was affected by varying moisture and fertility treatments. It increased as moisture level increased and decreased as fertility level increased. Values for German and Swedish origins were approximately constant at different moisture and fertility treatments. As a result, differences were found when shoot-root ratios were calculated using weights as opposed to those calculated using lengths. Based on weights, shoot-root ratios were most favorable for the Swedish origin and most unfavorable for the German. When lengths were used, ratios were best for the German and Swedish origins and most unfavorable for the Spanish provenance. This factor could be quite important in evaluating the effects of cultural treatments on growth and seedling balance.

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James Harold Brown

Candidate for the degree of

Doctor of Philosophy

Place of birth:

Richwood, West Virginia

Date of birth:

November 9, 1931

Marital status:

Married Yvonne Ann Beery, October 10, 1953

Children:

Sharon Lee Brown, born July 4, 1960

Education:

West Virginia University, BSF, 1953
Yale University, MF, 1954
Michigan State University, Ph. D., 1967

Experience:

Research Assistant, Northeastern Forest Experiment Station, Summer 1952, Summer 1953, June 1954 to March 1955
U. S. Army, March 1955 to March 1957 (Counter Intelligence Corps)
Assistant Silviculturist, West Virginia University Agricultural Experiment Station, April 1957 to June 1961
Assistant Professor of Silviculture, Division of Forestry, West Virginia University and Assistant Silviculturist, West Virginia University Agricultural Experiment Station, July 1961 to July 1967

Honorary societies:

Xi Sigma Pi
Alpha Zeta
Gamma Sigma Delta
Sigma Xi

APPENDIX

LIST OF COMMON AND SCIENTIFIC NAMES OF FOREST TREE SPECIES

Common Name	Scientific Name
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
larch, European	*Larix decidua* Mill.
pine, Corsican	*Pinus nigra* Arnold var. *poiretiana* (Ant.) Schneider
pine, jack	*Pinus banksiana* Lamb.
pine, loblolly	*Pinus taeda* L.
pine, lodgepole	*Pinus contorta* Dougl.
pine, longleaf	*Pinus palustris* Mill.
pine, pitch	*Pinus rigida* Mill.
pine, ponderosa	*Pinus ponderosa* Laws.
pine, red	*Pinus resinosa* Ait.
pine, Scotch	*Pinus sylvestris* L.
pine, shortleaf	*Pinus echinata* Mill.
pine, slash	*Pinus elliottii* Engelm.
pine, Virginia	*Pinus virginiana* Mill.
pine, white	*Pinus strobus* L.
spruce, Norway	*Picea abies* (L.) Karst.
spruce, Sitka	*Picea sitchensis* (Bong.) Carr.