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JAMES H. BROWN

NUMEROUS STUDIES have shown that survival varies when tree seedlings are transplanted at different times of the year. In general, these studies have shown that survival is lowest when transplanting is done during the period when top growth is most active. Drought has been cited as the major reason for seedling mortality and this has been related to inability of seedling root systems to supply moisture as rapidly as it is lost from the tops. The inability to supply sufficient moisture is caused, in part, by greater intake and loss of water during the period when height growth is most active (Kramer, 1932 and 1943; Kozłowski, 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).

Studies have also shown that there are decided differences in the seasonal height growth patterns of different provenances of the same tree species. 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. 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.

The purposes of the study reported here were: (1) to investigate the interrelationships between top growth, root growth and root regeneration potential of seedlings of different Scotch pine provenances:

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and (2) to study variations in survival of seedlings of those provenances when transplanted with different intensities of root pruning at different times of the year.

Procedure

Five seed sources of Scotch pine were selected, representing a north-south gradient through western Europe (Table 1). These seed lots were originally collected for use in the Scotch pine provenance study conducted by Wright and Bull (1963). Seed was sown in the Michigan State University Forestry 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 subjected to each of three intensities of root-pruning — removal of all lateral roots over three millimeters in length; removal of half the lateral root system; and removal of no roots. In removing half the lateral root system, laterals were spread out to their full extent and individual laterals were cut at approximately their midpoint.

After root-pruning, each seedling was transplanted into an individual container and the roots were covered with a potting mixture consisting of 2/3 (by volume) 20- to 40-mesh quartz sand and 1/3 shredded peat moss. This mixture contained complete fertilizer sufficient to provide 50 ppm N, 25 ppm P_2O_5 , and 50 ppm K_2O . The seedlings were placed in a greenhouse in the same order as in the nursery beds.

TABLE 1
Location and Climate at Place of Origin of Scotch Pine Provenances Used in Study

MSFG No. and Country of Origin (a)	Variety (b)	Location			Avg. Annual Temp.	Mos. Above 6° C	Annual Precip.
		Lat. N	Long. E	Elev. feet			
218	SPain	<i>iberica</i>	40.0	-5.3	3700	10.0	7 366
240	FRance	<i>aquitana</i>	42.6	2.1	4700	5.9	6 799
251	GERmany	<i>haguenensis</i>	49.1	8.1	500	9.9	7 536
550	S-SWEden	<i>rigensis</i>	55.9	14.1	100	6.9	6 468
548	N-SWEden	<i>lapponica</i>	63.5	18.7	700	2.0	4 568

(a) Numbers are those used in the Michigan State Forest Genetics accession record and are the same as those reported by Wright and Bull (1963) and Wright *et al.* (1966).

(b) Scotch pine varietal designations as assigned to these provenances by Ruby (1964).

They were watered sufficiently to maintain moisture in the potting mixture at a level slightly below field capacity. After 30 days, trees were removed from the pots and the root systems were carefully washed. Measurements were made on survival, top length, total lateral root length, and absorbing lateral root length. Absorbing lateral length was defined as the white 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 the seedlings were in the greenhouse.

Lifting from the nursery, root-pruning and transplanting were 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 source as the sub-plot effect, and intensity of root pruning as the sub-sub-plot effect, with two-tree plots replicated four times.

Statistical analyses for all data were made for three of the variables measured — survival, top length, and absorbing lateral root length. Analyses of total lateral root length were made only for seedlings transplanted in September, October, and November with no root-pruning. High mortality after July and August transplanting resulted in many missing plots.

Results

SURVIVAL

Survival varied significantly due to time of transplanting, seed source, and treatment (Table 2; Appendix Table 1). Survival was low for all trees transplanted in mid-summer, especially for those which suffered the most drastic root pruning. Survival was higher for trees transplanted in September and nearly 100 per cent for trees transplanted later.

There were significant (1 per cent level) time-seed source interactions. Seedlings of the three most southerly origins (SPA, FRA, and GER) had very low survival after transplantings in July and August and achieved 100 per cent survival only after November transplantings. Seedlings of the two Swedish origins had appreciably better survival in midsummer and reached 100 per cent survival after October lifting.

When seed sources were considered independently of time of transplanting, the north-Swedish source had significantly more (67 per cent) living trees than other sources. The south-Swedish origin had the next highest survival (57 per cent). Average survival of the three southern sources was 46 to 47 per cent.

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

TABLE 2

Survival and Height of Scotch Pine Provenances One Month After Transplanting With Various Intensities of Root Pruning

Date of Lifting	MSFG No. and Origin	Survival after removal of the following portion of lateral roots present at the time of lifting			Height (a)
		None	Half	All	
		per cent			mm.
July 20	218 SPA	12	12	0	31
	240 FRA	12	12	0	26
	251 GER	0	12	0	31
	550 S-SWE	25	12	0	30
	548 N-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 S-SWE	38	25	0	54
	548 N-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 S-SWE	75	75	0	70
	548 N-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 S-SWE	100	100	100	71
	548 N-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 S-SWE	100	100	100	70
	548 N-SWE	100	100	100	53

(a) There were no significant differences in height for seedlings receiving different intensities of root pruning.

one-half root removal had low survival from July and August transplantings. In later liftings, the number of living trees increased, reaching 100 per cent in October and November. For trees having full-root pruning, there was no survival (except for N-SWE) until after the October transplanting.

TOP GROWTH

Most top growth occurred before transplanting, therefore it was affected significantly by time of measurement, seed source, and time-seed source interaction. There were no significant differences between seedlings receiving different intensities of root pruning (Table 2; Appendix Table 1).

Top growth was completed in all five seed sources by September 20. As shown in Figure 1 and Tables 2 and 3, the German provenance had a relatively rapid and constant growth rate throughout the height growth period. Approximately one-third of the total elongation occurred during each of the three months preceding September 20. Seedlings from northern Sweden had a decidedly different pattern. Over one-half of the total growth was completed by July 20 and over 80 per cent was completed by August 20. Growth patterns of the other three sources were similar, with 43 per cent of total elongation completed by July 20 and approximately 75 per cent completed by August 20.

German seedlings grew 100 mm. tall, almost 30 mm. more than the next best sources from Spain and southern Sweden. Total top growth for the French source was about 60 mm., while the maximum attained by north-Swedish seedlings was a little over 50 mm.

TOTAL LATERAL ROOT LENGTH

Only data for those trees which received no root pruning and were transplanted from September to November were analyzed statistically (Appendix Table 2). Differences due to time of transplanting, seed source, and time-seed source interaction were significant. 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 3, 4; Figure 1.)

Although data for July and August transplantings were not analyzed statistically, there were probably time-seed source interactions (Figure 1). The two Swedish provenances had the greatest total lateral root lengths after the first transplanting, while roots of German seedlings were longest after later transplantings. Spanish and French trees produced few lateral roots in the early months and did not catch up to the north-Swedish trees until October. Roots of October transplanted trees of all provenances were 90 to 97 per cent as long as those of November transplanted ones; there were no significant time-seed source interactions for these months.

Figure 1. Height and total lateral root length for five provenances of Scotch pine transplanted with no root pruning at five different times.

Roots of German seedlings had a maximum total lateral length which was nearly 70 per cent more than for the source (S-SWE) with the next longest lateral root length. Spanish and French seedlings had total lateral lengths of about 400 cm., while trees from northern Sweden attained a maximum lateral extent of 340 cm.

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 exist-

TABLE 3
Percentage of End-of-Season Growth Attained at Various Measurement Dates (30 Days After Lifting Dates)

MSFG No. and Origin	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
				Per cent 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 S-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 N-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

ing 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 2). Also, all second- and third-order interactions were significant (Appendix Table 1). There was very little new lateral root elongation on any provenance transplanted in July and August. Growth became progressively greater after September and October transplanting and then leveled off in November. All monthly differences except the July-August and October-November comparisons were significant.

TABLE 4

Lateral Root Length of Scotch Pine Provenances One Month After Transplanting With Various Intensities of Root Pruning

Date of lifting	MSFG No. and origin	Length of lateral roots after removal of the following portions of laterals:					
		Total Length			Absorb. Length		
		None	Half	All	None	Half	All
centimeters							
July 20	218 SPA -----	4	6	—	2	3	—
	240 FRA -----	5	1	—	5	1	—
	251 GER -----	—	4	—	—	2	—
	550 S-SWE -----	32	2	—	8	2	—
	548 N-SWE -----	44	21	—	10	13	—
Aug. 20	218 SPA -----	21	17	—	8	10	—
	240 FRA -----	—	19	—	—	10	—
	251 GER -----	65	—	—	15	—	—
	550 S-SWE -----	46	19	—	14	14	—
	548 N-SWE -----	63	38	15	20	24	15
Sept. 20	218 SPA -----	108	146	—	38	100	—
	240 FRA -----	125	115	—	49	80	—
	251 GER -----	264	149	—	88	89	—
	550 S-SWE -----	188	158	—	62	107	—
	548 N-SWE -----	142	82	27	32	48	26
Oct. 20	218 SPA -----	393	360	30	100	168	27
	240 FRA -----	362	319	50	92	152	43
	251 GER -----	1125	878	98	265	390	90
	550 S-SWE -----	642	599	59	178	282	55
	548 N-SWE -----	308	228	44	60	95	40
Nov. 20	218 SPA -----	414	332	50	98	155	46
	240 FRA -----	408	338	34	103	170	50
	251 GER -----	1162	900	90	256	405	86
	550 S-SWE -----	685	580	58	181	288	53
	548 N-SWE -----	345	226	40	62	97	38

There were pronounced differences among sources in the total length of absorbing laterals produced by the end of the season (November). German seedlings had the greatest absorbing lateral root extent. South-Swedish ones had the next greatest amount and north-Swedish trees the least (Table 4; Figure 2). Root pruning affected the actual length of absorbing laterals produced but did not affect the ranking of seed sources.

Figure 2. Length of absorbing (white) roots of Scotch pine as affected by date of transplanting, intensity of root pruning at transplanting time and provenance.

The ranking of seed sources did vary with transplanting date. North-Swedish trees had the longest absorbing laterals after the July and August transplantings and the least amount of absorbing laterals from September on. German seedlings had intermediate absorbing lateral lengths after the first two transplantings but the greatest amount for trees transplanted in September or later.

Average length of absorbing laterals was significantly affected by intensity of root pruning. It was greatest on trees receiving half-root pruning and least on those which were fully root-pruned (Table 4; Figure 2). Treatment-time and treatment seed-source interactions were also significant. For trees transplanted in July and August, absorbing lateral lengths were approximately the same for trees which had lost half their laterals as for those which had not been root pruned. After October and November transplantings absorbing lateral lengths were approximately 50 per cent greater if trees had lost half their laterals than if no root pruning had been done. Increases in absorbing lateral lengths on half root-pruned trees were least (45 per cent) for German and north-Swedish trees and greatest (75 per cent) for the French and Spanish provenances.

Discussion and Conclusions

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 1). Nearly half the total root elongation occurred during September and October on trees from north-Sweden. During that same period the proportion of total root growth was approximately 60, 66, and 70 per cent, respectively, for trees from France, south-Sweden and Spain. Trees from Germany had the highest percentage of total root growth during this interval; 72 per cent 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 heights 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

Survival was closely correlated with the length of the root system at the time of transplanting and the growth of new roots after transplanting. During the early part of the growing season root lengths were very low and neither the length 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 seedlings from northern Sweden survived even moderately well and that was the origin with the largest root system at time of transplanting and the most root growth during the subsequent months.

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. As transplanting was done later in the fall, the amount of lateral growth increased and height growth decreased. Survival of trees transplanted in October and November was 100 per cent for all trees which had no or half-root pruning. Trees with all laterals removed at transplanting time could produce relatively little new root growth in the subsequent month and did not survive well except after the last transplanting.

Time of completion of height growth also apparently affected survival. Seedlings from northern Sweden survived as well or better than those of all other sources after all treatments and times of transplantings although they had the most lateral roots 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 intake and loss for north-Swedish trees apparently counter-balanced their relatively small root systems.

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 per cent in the autumn. This is similar to the trend found in this study in which seedlots from the coolest climates developed the highest survival potential earliest in the season.

RECOMMENDATIONS FOR FIELD PRACTICE

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, 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 might be questionable. A number of studies, including those of Addoms (1946) and Kramer (1946), 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. 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.

Summary

Nursery grown seedlings of five provenances of Scotch pine from widely separated portions of the species range in western Europe 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 between provenances in seasonal patterns of 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 neither the amount of root present at transplanting nor new growth after transplanting was sufficient to supply moisture to 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.

Seasonal patterns of survival and root growth were closely correlated with the provenances used. After July and August transplantings, survival was somewhat better for seedlings from northern and southern Sweden. These provenances were also found to have the most rapid initial rates of root growth and root regeneration. Survival of seedlings from north-Sweden reached 100 per cent after the September transplanting and after the October transplanting for the other provenances.

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.

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APPENDIX

APPENDIX TABLE 1

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	Height
Replication	3	—	—
Date of lifting	4	572.0**	370.6**
Error a	12	—	—
Seed Source	4	13.8**	409.3**
Source x Date	16	3.0**	32.9**
Error b	60	—	—
Treatment	2	59.8**	2.9
Treatment x Date	8	7.8**	.5
Treatment x Source	8	1.6	.2
Treatment x Date x Source	32	1.4	.4
Error c	150	—	—

** Significant at 1 per cent level.

APPENDIX TABLE 2

Analyses of Variance for Total Length of Lateral Roots 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
		F ratio
Replication	3	—
Date of lifting	2	105.3**
Error a	6	—
Seed Source	4	89.3**
Source x Date	8	12.6**
Error b	36	—
Treatment	1	—
Treatment x Date	2	—
Treatment x Source	4	—
Treatment x Date x Source	8	—
Error c	45	—

(a) Due to high mortality after the July and August transplantings this variable was analyzed for only a portion of the data.

** Significant at 1 per cent level.