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Effect of rootstock and scion on flowering, growth and foliar nutrients of loblolly pine (*Pinus taeda*) grafts

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TIIVISTELMÄ: PERUSRUNGON JA VARTTAMISOKSAN VAIKUTUS PINUS TAEDAN VARTTEIDEN KUKINTAAN, KASVUUN JA NEULASTEN RAVINNEPITOISUUTEEN

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In two separate studies, seedlings from 20 loblolly pine families and Virginia pine were used as rootstocks for grafting loblolly pine seed orchard clones. The rootstocks were open-pollinated seedlings from orchard clones chosen to represent a wide range of flowering and survival capabilities, based on their performance in a first-generation seed orchard. Scions were derived from the same 20 loblolly clones. The effects of scion clone were significant and large for nearly all measured traits. Rootstock significantly affected survival, growth, flowering and foliar nutrients of the grafted ramets. Neither survival nor growth of the grafts was related to survival or growth of the orchard clones from which their rootstocks were derived, however. Survival of incompatible clones was enhanced by grafting on genetically related rootstock.

Kahdessa erillisessä kokeessa käytettiin *Pinus taedan* siemenviljelyskloonien varttamisessa perusrunkoina siementaimia 20:sta *P. taedan* jälkeläistöstä sekä *P. virginianan* siementaimia. Perusrungot olivat sellaisten siemenviljelyskloonien jälkeläisiä, jotka oli valittu ensimmäisen polven siemenviljelyksissä ilmenneiden elävyys- ja kukkimisominaisuuksien perusteella. Varttamisoksat otettiin samoista *P. taeda* -klooneista.

Lähes kaikissa ominaisuuksissa oli merkitseviä ja suuria eroja eri kloonien välillä. Perusrunko vaikutti merkitsevästi vartteiden elävyyteen, kukintaan ja neulasten ravinnepitoisuuteen. Elävyys ja kasvu eivät kuitenkaan olleet suhteessa niiden kloonien vastaaviin ominaisuuksiin, joista perusrungot polveutuivat. Vaikeasti vartettavien kloonien elävyys parani, kun ne vartettiin lähisukuisiin perusrunkoihin.

Keywords: grafting, incompatibility, genetics.
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1 Introduction

Seed orchards of southern pines are usually established by grafting scions from superior phenotypes on seedling rootstocks. Over 4000 ha of seed orchards have been established in this manner in the southeastern United States (Jett 1988). In general, grafted orchards have been quite successful, but problems such as poor survival and low seed production still exist, especially for some clones. In grafted loblolly pine seed orchards, the scion clone has major effects on fruitfulness of the grafted ramet (Schmidtling 1974), which leads to a wide disparity among clones in their genetic contribution to the orchard output (Schmidtling 1983b).

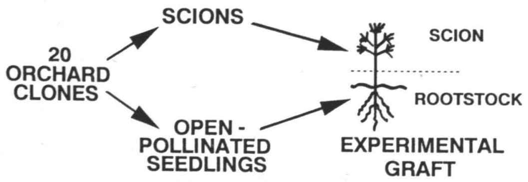
In some older orchards, seed production has been adequate, but the ramets have become too large for efficient harvesting. It is possible that the choice of proper rootstocks could ameliorate all of these problems.

Selected rootstocks have been used in fruit trees for more than a century to increase fruit production and limit tree size (Sax 1958). Jayawickrama et al. (1991) have recently reviewed the literature with regard to rootstock effects in conifers. Rootstocks have been shown to influence a wide range of characteristics such as growth, survival, fruitfulness and mineral nutrition in conifers.

The present study seeks to identify suitable rootstocks for use in loblolly pine (*Pinus taeda* L.) seed orchards, and to determine what *a priori* characteristics can be used to identify such rootstocks. The study also explores the effects of rootstock and scion on mineral nutrition as it relates to growth and flowering.

2 Materials and methods

Two studies were established using material from a loblolly pine seed orchard in south Mississippi. Clones were selected from the orchard to represent a wide range of compatibility and fruitfulness. In both studies, open-pollinated seed were collected from orchard ramets, sown in the nursery the following spring, and placed into pots the following winter for use in grafting. Scions were collected from the same orchard source the following January, top-cleft grafted onto the potted seedlings, and outplanted in the fall following grafting:



2.1 The HEF study

The first study was established on the Harrison Experimental Forest (HEF study) in south Mississippi approximately 30 km north of the Gulf Coast. Sixteen scion clones were grafted onto nine open-pollinated rootstock families (Table 1) in a factorial combination. The survivors were planted at 5 m × 5 m spacing in a completely random design in the fall of 1978. Since many of the same clones were used for both rootstock and scion, nine of the scion/rootstock combinations involved genetically related partners. Grafting success was poor, and many scion/rootstock combinations were missing. Scion clones and rootstock families with the fewest individuals were sequentially dropped from the data set until a balanced sub-set was obtained for analysis of all traits except survival. There is a possible bias introduced by this practice, if any of our other traits are strongly related genetically to survival. This is probably not important, however, since most early failures were due to poor grafting technique. In a practical sense, we are not very interested in scion clones or rootstock families with poor survival.

Heights of the ramets were measured in 1983, 1987, and 1991. Female strobili were counted in the spring of 1984 through 1991. Male strobili clusters were counted in 1988, 1990 and 1991.

In September of 1989 and again in 1990, foliar samples were collected from 93 random sample trees representing a factorial combination of seven scion clones and five rootstock families. The selection of the scion clones and rootstock families was largely governed by the number of survivors of each combination. Needles from the last-formed flush were collected from three branch tips in the upper crown of each tree, oven dried and sent to a commercial agricultural laboratory for analysis of nitrogen (N), phosphorous (P), potassium (K), sulfur (S), magnesium (Mg), calcium (Ca), iron (Fe), aluminum (Al), manganese (Mn), boron (B), copper (Cu), and zinc (Zn) content.

Table 1. Numbers of surviving grafts outplanted in the fall of 1978 at the Harrison Experimental Forest (HEF study) in south Mississippi.

Rootstock family	Scion clone																
	1	2	4	5	6	7	8	9	10	14	18	24	25	29	31	49	Total
1	3[1]	-	3	-	-	3	-	-	-	-	-	-	-	-	-	-	9
2	-	1	-	2	2	-	1	-	3	-	-	3	4	4	3	4	27
4	-	-	8	-	-	1	-	2	-	1	2	-	-	4	-	-	18
5	-	2	-	2	2	-	1	-	2	-	-	2	5	8	3	5	32
6	-	3	-	1	1	-	3	-	2	-	-	1	2	3	3	3	22
8	-	3	-	-	1	-	2	-	4	-	-	3	2	3	2	3	23
9	5	-	5	-	-	4	-	6	-	1	4	1	-	6	-	-	32
10	-	4	-	4	1	-	1	-	1	-	-	3	4	1	4	2	25
14	2	-	-	-	-	1	-	-	-	3	4	-	-	4	-	-	14
Total	10	13	16	9	7	9	8	8	12	5	10	13	17	33	15	17	202

[1] Underlined numbers indicate that the scion and rootstock are related genetically.

Table 2. Surviving grafts planted in the spring of 1983 at the Erambert Seed Orchard (Erambert study) in south Mississippi.

Rootstock family	Scion clone															
	2	4	5	10	11	14	20	23	25	31	33	36	37	40	Va[1]	Total
4	2	2[2]	2	3	2	3	2	2	3	1	2	3	3	1	6	37
10	3	1	2	5	3	3	2	3	2	3	2	3	3	3	5	43
11	3	2	2	1	2	3	2	3	2	1	2	1	2	3	5	34
13	2	3	3	3	2	3	1	2	3	-	2	3	3	3	8	41
14	2	3	2	3	3	5	2	4	1	3	3	2	3	3	7	46
20	3	3	2	3	3	3	9	3	3	2	3	2	2	3	12	56
25	2	3	3	3	3	3	2	2	3	3	1	3	3	3	9	46
31	2	3	3	3	1	2	2	2	3	6	2	2	1	2	3	37
37	2	3	3	3	3	3	3	2	3	2	3	3	7	3	11	54
40	2	2	3	3	3	3	3	2	3	2	3	3	2	3	9	75
Total	23	25	25	30	25	31	28	25	26	23	23	25	29	27	75	440

[1] Virginia pine rootstock.
[2] Underlined numbers indicate that the scion and rootstock are related genetically.

2.2 The Erambert study

The second study was established at the Erambert Seed Orchard (Erambert study), a USDA-Forest Service seed orchard located in southern Mississippi about 100 km north of the Gulf Coast. Ten loblolly pine scion clones were grafted onto 14 open-pollinated loblolly rootstock families plus Virginia pine (*Pinus virginiana* Mill.) rootstock in a factorial arrangement (Table 2). The Virginia pine rootstock was included because it showed promise as a rootstock for loblolly pine grafts in a previous study (Schmidtling 1983a). Seed for the Virginia pine rootstock was collected from an orchard in western North Carolina. Five rootstock families and five scion clones were common to both studies.

The surviving grafts were planted in March of 1983 at 5 m × 10 m spacing in a completely random design. Although grafting success was much better in the Erambert study, it was still necessary to use a sub-set of the data for analysis of all traits except survival, as in the HEF study.

Heights of the ramets were measured in 1985, 1987, and 1991. Female strobili were counted in the spring of 1984 through 1991. Male strobili clusters were counted in 1991.

In September of 1987, foliar samples were collected from 136 trees randomly selected to represent a factorial combination of eight scion clones and seven rootstocks, including Virginia pine rootstocks. In 1988, foliar samples were collected from 122 trees representing a factorial combination of seven scion clones and seven rootstocks, including Virginia pine rootstocks. Samples were collected and analyzed the same as in the HEF study.

2.3 Statistical analysis

The analysis of variance for the quantitative data has the form:

Factor	Degrees of freedom
Scion	s
Root	r
Scion × root	rs
Error	n-r-s-rs-1

The fixed model was assumed. Since the number of entries per cell is variable, the SAS General Linear Model Procedure (GLM) (SAS user's... 1985) was used. The 0.05 level of probability was used to test significance, except for the mineral composition data, where the exact probabilities are tabulated. The square-root transformation was used for strobili counts to stabilize variance. In the Erambert study, a preplanned comparison of Virginia pine rootstock versus the mean of the loblolly rootstocks was tested in the analysis of variance for each trait.

Regression was used to compare performance of rootstocks with the performance of the scion clones from which they were derived. This was done to determine if the performance of a clone in an orchard could be used to predict survival, growth, and flowering when seedlings from these clones were used as rootstock. Multiple regression, multivariate analysis of variance and canonical discriminant analysis was used to explore multivariate relationships in foliar nutrients among scions, rootstocks and individual grafts. Survival data were analyzed using Chi-square contingency tables.

3 Results and discussion

3.1 Survival

Overall survival after outplanting in the HEF study was good, with 81 per cent surviving after 13 years. There was significant variation among scion clones, as well as among rootstock families in chi-square tests (Table 3). Survival of scion clones ranged from 20 per cent for clones 1 and 7, to 100 per cent for several clones. Survival by rootstock was not as variable, ranging from 59 per cent for family 14 to 100 per cent for family 16.

Overall survival after outplanting in the Erambert study was slightly lower than in the HEF study, with only 72 per cent surviving. Variation among scion clones was similar to that observed in the Erambert study, ranging from 21 per cent for clone 14 to 95 per cent for clone 4 (Table 4). Rootstock survival ranged from 56 per cent for family 23 to 89 per cent for family 20. Survival of grafts on Virginia pine rootstock was 65 per cent, less than the average of 72 per cent. Loblolly and Virginia pine are both hard pines, but are not very closely related taxonomically, as loblolly belongs to the Australes Subsection whereas Virginia pine belongs to the Contortae Subsection (Critchfield and Little 1966). Survival of grafts on Virginia pine rootstock, however, was as good or better than grafts on three of the loblolly rootstocks, families 2, 23, and 33. Interspecific grafting of pines has sometimes been very successful, and other times a complete failure (Jayawickrama et al 1991). Virginia pine rootstocks, however, have previously been used successfully for loblolly pine scions (Schmidtling 1983a).

Table 3. Survival, flowering (eight year average) and 13-year heights of loblolly pine grafts when seed orchard clones were used as scions, and open-pollinated seedlings from the clones were used as rootstock (HEF study).

	When used as a rootstock			When used as a scion clone		
Family	Survival	Height	Female flowering	Survival	Height	Female flowering
	%	m	no	%	m	no
1	78	10.24	13.1	20	12.65	6.2
2	89	10.21	13.9	100	10.45	5.5
4	83	10.42	15.0	100	10.79	8.1
5	88	10.51	13.3	78	10.18	12.9
6	91	10.12	12.0	100	11.28	6.4
7	-	-	-	20	10.52	3.8
8	96	10.24	14.5	100	9.54	14.7
9	59	10.73	18.3	87	11.16	27.0
10	84	10.48	14.9	100	8.81	4.1
14	57	10.17	7.1	80	12.83	13.4
16	100	9.04	13.4	-	-	-
18	-	-	-	40	9.88	4.3
24	-	-	-	38	10.06	8.1
25	-	-	-	100	10.15	0.5
29	-	-	-	88	8.90	15.8
31	-	-	-	100	8.99	8.3
49	-	-	-	94	10.09	0.6

Table 4. Survival of loblolly pine grafts when seed orchard clones were used as scions, and open-pollinated seedlings from the clones were used as rootstock (Erambert study).

Family ID	Survival as a rootstock %	Survival as a scion %
2	61	-
4	72	95
5	76	-
10	83	91
11	72	21
13	-	71
14	74	22
20	89	71
23	56	-
25	88	93
31	78	81
33	65	-
36	72	-
37	72	85
40	70	87
Va pine	65	-
Average	72.5	

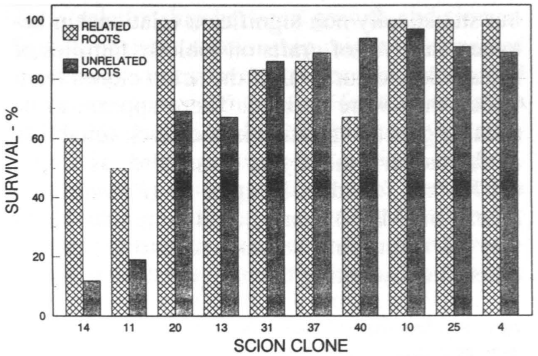


Fig. 1. Survival of loblolly pine ramets grafted on genetically related rootstocks compared to survival on unrelated rootstocks in the Erambert study.

There did seem to be some advantage to grafting scions onto genetically related rootstock. In the HEF study, 94 per cent of scions grafted on related rootstock survived, versus 85 per cent on unrelated rootstock. The advantage of grafting on related rootstock was a little greater in the Erambert study, where survival was 87 per cent on related rootstock versus 72 per cent on unrelated rootstock.

In examining the variation in survival by scion clone in the Erambert study, it is clear that this advantage does not obtain equally for all clones (Fig. 1). When the survival data of related versus unrelated rootstock is separated by scion clone, survival differences were significant for only two clones. Survival of clones 14 and 11 which was less than 20 per cent on unrelated rootstock, was increased nearly three-fold by grafting on related rootstocks. The advantage of related rootstock is very small and not statistically significant for the clones with better overall survival such as clones 31, 37, 10, 25, and 4. Survival on related rootstock was actually poorer for clone 40, but the numbers were small and the difference was not statistically significant.

The advantage to using related rootstock, therefore, depends on the magnitude of the survival problem in a given clone. There seems to be great advantage in grafting incompatible clones on related rootstock, as shown by Slee and Spidy (1970), but little advantage in using related rootstock on clones where compatibility is not a problem (Schmidtling 1986).

In both studies, there was a weakly positive, but statistically non-significant relationship between survival of grafts on loblolly families of rootstock and survival of the scion clones from which they were derived. There appears to be useable genetic variation in rootstock suitability as far as survivability is concerned, as Copes (1974) has found in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), but there may be no way of identifying suitable rootstock families other than by testing them in rootstock trials.

3.2 Height

In both studies, height varied significantly by scion clone as well as by rootstock family. The scion × rootstock interaction was not significant in either study.

Variation among scion clones in height was much greater than among rootstocks in the HEF study (Table 3). Height of clone 14 averaged 12.83 meters compared to only 8.9 meters for clone 29. The range in heights by rootstock was from only 9.04 for family 16 to 10.51 meters for family 5.

The Erambert study included Virginia pine rootstocks with the expectation that this rootstock would have a growth limiting effect. Fig. 2 shows that this rootstock has performed according to expectation. Heights of grafts ranged from 7.4 m on family 23 rootstocks to less than 6.3 m on Virginia pine rootstocks. Grafts on rootstock families 36 and 40, however, were almost as short as those on Virginia pine rootstocks. Grafting loblolly pine scion clones on Virginia pine rootstock resulted in a statistically significant reduction in height growth of 10 per cent below the average for loblolly rootstocks, which is comparable to the height reduction found in a previous study (Schmidtling 1983a).

There was no obvious relationship between growth and survival of the grafts on various rootstocks. Growth of grafts on Virginia pine rootstocks was the slowest (Fig. 2), and survival was below average (Table 4), which might indicate that the dwarfing effect was due to a partial incompatibility. The growth-retarding effect of loblolly rootstocks 36 and 40 was equivalent to Virginia pine, however, and survival was average on these rootstocks. The tallest grafts were those on loblolly rootstock 23 at nearly 7.5 m, but they also had the poorest survival at 56 per cent.

Grafting loblolly scions on genetically related rootstock had little effect on growth. As in a previous study with slash pine, grafts on related rootstock averaged slightly taller than on unrelated rootstocks (Schmidtling 1986), but in this study the differences were not statistically significant.

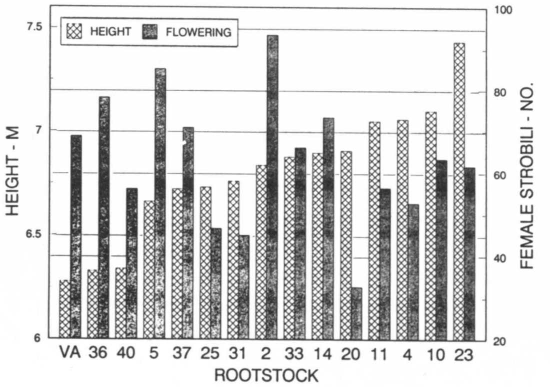


Fig. 2. Height and flowering of loblolly pine ramets grafted on Virginia pine rootstocks and on 14 open-pollinated loblolly pine rootstock families.

There was no relationship in either study between growth of the scion clones and growth of the graft when seeds from these scion clones were used as rootstock (Table 3). Seedling rootstocks derived from slow-growing clones do not cause slower growth of a graft when used as a rootstock. One could not use the growth of a clone in an orchard as an indicator of performance of seedlings from that clone as rootstock, with regard to height growth.

3.3 Flowering

Flowering is a highly heritable trait in loblolly pine, with clonal heritabilities averaging around 0.5 (Schmidtling 1983b), so it is not unexpected that scion effects for numbers of strobili were statistically significant every year in both studies. Flowering of the scion clones in the HEF study varied widely, from 0.5 strobili per year per ramet for clone 25 to 27.0 strobili per year per ramet for clone 9 (Table 3).

Rootstock effects in the Erambert study were consistently significant from year to year. The eight-year average for number of female strobili varied widely, from 30 strobili per year per ramet on family 20 rootstock to over 90 on rootstock 2 (Fig. 2). Flowering of ramets on Virginia pine rootstock was considerably above average, even though these grafts were the shortest.

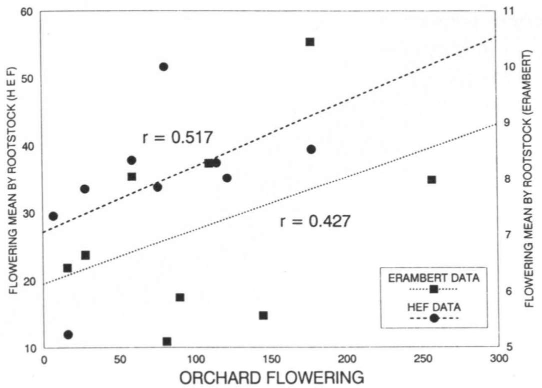


Fig. 3. Flowering performance of open-pollinated loblolly pine families when used as rootstock compared to flowering of the orchard clones from which they were derived.

The effects of rootstock on flowering in the smaller HEF study, on the other hand, were statistically significant only two years out of eight (at $p = 0.05$). The range of variation among rootstocks was much less than among scions, ranging from 7.1 strobili per ramet per year for family 14, to 18.3 for family 9 (Table 3).

Grafting loblolly pine scions onto genetically related rootstock had very little effect on flowering. As in a previous study in slash pine (Schmidtling 1986), grafts on related rootstock averaged slightly fewer female strobili than on unrelated rootstock, but the differences were small and statistically insignificant.

In the earlier flowering data (through 1988), there was a positive relationship between flowering performance of the scion clones, and flowering performance when seedlings from these clones were used as rootstock (Fig. 3). This would seem to indicate that one should use seed from the best flowering clones in an orchard for use as rootstock in future seed orchards. It is difficult to justify such a relationship, unless flowering is influenced by some genetically variable factor, such as gibberellin, which is produced in the entire tree and can be transported from root to scion. In any case, this positive relationship did not obtain in the later flowering data.

There was no obvious relationship between growth and flowering in either study (Fig. 2, Table 3). There are two opposing expectations for a relationship between growth and flowering. A positive relationship might be expected since larger trees have a greater crown area, and therefore more potential sites for the formation of female strobili. In loblolly pine orchard ramets of the same age, there is a positive relationship between diameter and cone production (Schmidtling 1983b). A negative relationship could also be expected, because vigorous vegetative growth may be carried on at the expense of reproductive growth (Greenwood 1978).

A combination of the two relationships may be more realistic. In an earlier study, grafting loblolly pine scions on Japanese red pine (*Pinus densiflora* Sieb and Zucc.) rootstocks resulted in a 20 per cent reduction in growth and doubling of female production through the first five years, compared to scions grafted on loblolly pine rootstocks (Schmidtling 1983a). The flowering of the grafts on Japanese red pine rootstock was only average after the first five years, however, because of the much smaller size of these grafts.

3.4 Foliar nutrients

Macro- and micronutrients varied from year-to-year within studies, and especially between the two studies (Tables 5 and 6). N, P, K and Mg averaged higher in the Erambert study than in the HEF study, reflecting the general superiority of the Erambert site. Ca and Mn averaged slightly higher in the HEF study.

There was considerable variation among years and studies in significance levels of scion and rootstock effects for the various nutrients (Tables 5 and 6). Generally, there was more significant variation among scion clones than among rootstock families (Tables 5 and 6). This is not unexpected, since it is genetic differences that are being measured. Each scion clone has all it's genes in common with all other ramets of the same clone. The open-pollinated rootstock families, however, are a mixture of half- and full-sibs. This means that any individual within a family has only 1/2 or 1/4 of it's genes in common with any other individual in the same family (Falconer 1981). Variation within a rootstock family would therefore be much greater than variation within a scion clone relative to environmental variation and error, if scion and rootstock affect mineral nutrition equally. Although rootstock effects are significant only 1/3 as frequently as scion effects in Tables 5 and 6,

Table 5. Average macro- and micronutrient contents and statistical significance of scion and rootstock effects on nutrient composition of loblolly pine needles in the HEF experiment. Sample size was 93 for both years. Probability values of 0.1 or less are flagged with "#" (SAS user's... 1985, GLM procedure).

		1989			1990		
Mineral	Avg. content	Scion	Rootstock	Scion × rootstock	Scion	Rootstock	Scion × rootstock
	%	Probability of no effect is less than					
N	1.32	0.085 #	0.531	0.890	0.005 #	0.255	0.158
S	0.06	0.492	0.778	0.191	0.014 #	0.827	0.377
P	0.15	0.798	0.710	0.695	0.100 #	0.951	0.074 #
K	0.85	0.027 #	0.345	0.749	0.168	0.096 #	0.696
Mg	0.12	0.001 #	0.478	0.947	0.001 #	0.973	0.684
Ca	0.22	0.026 #	0.019 #	0.423	0.006 #	0.396	0.300
	ppm						
Fe	48.5	0.001 #	0.112	0.315	0.007 #	0.123	0.199
Al	477	0.113	0.006 #	0.955	0.134	0.060 #	0.425
Mn	308	0.373	0.606	0.705	0.045 #	0.665	0.105
B	14.8	0.151	0.985	0.671	0.303	0.879	0.949
Cu	6.63	0.672	0.140	0.930	0.653	0.476	0.905
Zn	26.8	0.077 #	0.780	0.505	0.032 #	0.592	0.526

Table 6. Average macro- and micronutrient contents and statistical significance of scion and rootstock effects on nutrient composition of loblolly pine needles in the Erambert experiment. In 1987, 136 samples were analyzed, in 1988, 122 samples were analyzed. Probability values of 0.1 or less are flagged with "#" (SAS user's... 1985, GLM procedure).

		1987			1988		
Mineral	Avg. content	Scion	Rootstock	Scion × rootstock	Scion	Rootstock	Scion × rootstock
	%	Probability of no effect is less than					
N	1.05	0.012 #	0.018 #	0.826	0.372	0.965	1.000
S	0.05	0.104	0.318	0.812	0.061 #	0.268	0.962
P	0.07	0.117	0.936	0.992	0.005 #	0.213	0.729
K	0.48	0.001 #	0.084 #	0.840	0.001 #	0.112	0.426
Mg	0.20	0.008 #	0.072 #	0.651	0.062 #	0.001 #	0.823
Ca	0.32	0.006 #	0.376	0.693	0.001 #	0.722	0.936
	ppm						
Fe	54.5	0.057 #	0.529	0.297	0.001 #	0.025 #	0.248
Al	420	0.009 #	0.744	0.098 #	0.002 #	0.197	0.637
Mn	638	0.004 #	0.296	0.484	0.736	0.695	0.725
B	14.1	0.034 #	0.007 #	0.001 #	0.264	0.790	0.435
Cu	4.51	0.484	0.045 #	0.215	0.006 #	0.857	0.907
Zn	25.6	0.084 #	0.100 #	0.857	0.001 #	0.841	0.670

rootstock effects on foliar nutrition are probably as important as scion effects.

The levels of foliar nutrients did not seem to be closely related to either height or flowering. Multiple regressions of height or flowering as dependent variables and all of the foliar nutrients as independent variables were computed with the 1987 Erambert data on an individual tree basis. Only 14 per cent of the variation in height and 16 per cent of the variation in flowering was explained by the model.

Clonal means for N, K, Mg, Ca, Mn and B are compared to height and flowering in Fig. 4. There was considerable variation in all nutrients, but no obvious relationship with flowering or growth. Smith and Stanley (1967) found that better cone-producing slash pine (*Pinus elliottii* Engelm.) tended to have higher foliar N, but there was no evidence for a relationship between N contents of needles and female strobilus production in this experiment.

Genetic variation in foliar nutrients, especially at the clonal level, would certainly be expected for most minerals. It is also reasonable to assume that the concentration gradients created by metabolic activity in the foliage would be important in determining uptake by the root systems. It has long been known, however, that the accumulation of minerals by root systems is dependent on metabolic activities of plant cells within the roots (Hoagland 1937). Genetic variation in mineral uptake of the root systems should therefore be expected.

Rootstock appeared to be responsible for variation in many of the foliar nutrients measured (Table 5 and 6). Rootstock means for N, K, Mg, B, Zn, and Cu for the Erambert study in 1987 are compared to height and flowering of the same sub-sample in Fig. 5. Although there did not appear to be any obvious relationship between flowering (Fig. 5h) and rootstock variation in foliar nutrients, variation in height (Fig. 5g) was related to K concentration (Fig. 5e), at least superficially.

The lack of a relationship between N concentration and flowering is puzzling, since fertilization with N is nearly always effective in increasing female flower production in loblolly pine (Schmidtling 1974). In a slash pine study, rootstock effects on nitrogen were weakly related to female flowering in one scion clone in a two-clone experiment, but not in the other clone (Schmidtling 1988).

The Virginia pine rootstock appeared to be responsible for a substantial portion of the rootstock variation in the Erambert study. Besides being the shortest in height and the heaviest flowering (in the 1988 foliar sub-sample), the grafts on Virginia pine rootstock were the lowest in foliar K and Mg, second highest in N and B, and second lowest in Cu. In a canonical discriminant analysis including all the foliar nutrients, Virginia pine rootstock is the only rootstock that is at all distinguishable from the others in a plot of the first two canonical variables (Fig. 6).

The sub-sample used in the foliar analysis also included genetically related rootstock-scion combinations. There was no effect of relatedness on foliar nutrients. Having the scion related to the rootstock did not appear to facilitate the transfer of nutrients from the roots to the foliage.

3.5 Scion × rootstock interactions

In a multivariate analysis of variance of the foliar nutrients, rootstock effects and scion clone effects were significant at the 0.01 level in all analyses. The scion × rootstock interactions were also significant. This is of doubtful importance (and difficult to interpret), however, since the interactions in the univariate analysis of the foliar nutrients seldom approached significance (Tables 5 and 6). The interactions were also not significant in the analysis of flowering and growth variables. This is in contrast to other studies where rootstock × scion interactions were large enough to cloud the interpretation of the data (Schmidtling 1983a, 1988). These earlier studies, unlike the present studies, utilized only two or three widely contrasting scion clones. The interactions appear to be less important when a wide range of scion clones are utilized, which approximates more closely the situation in an operational orchard.

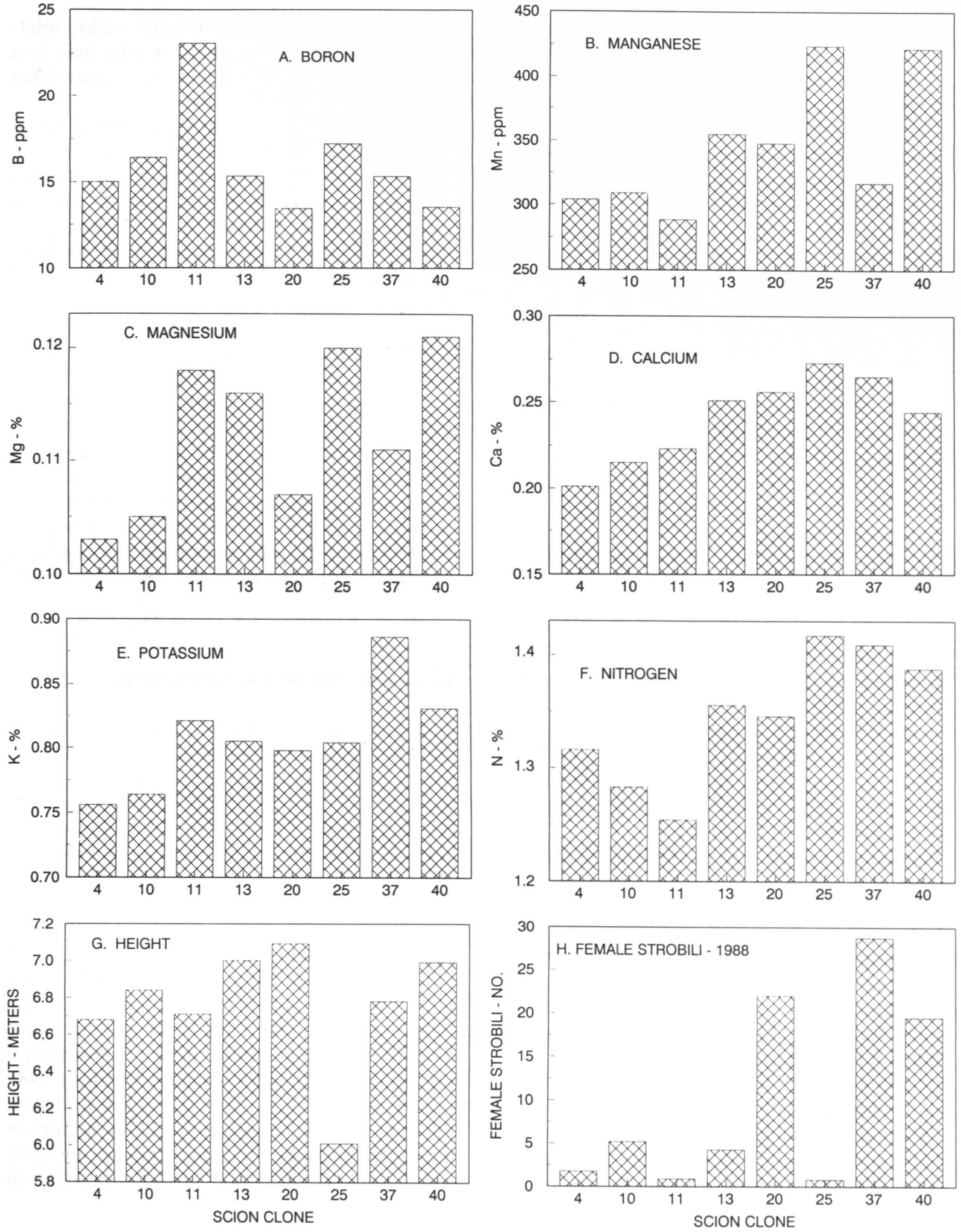


Fig. 4. Mean foliar concentrations by scion clone of several macro- and micronutrients compared to flowering and growth in the Erambert study in 1987.

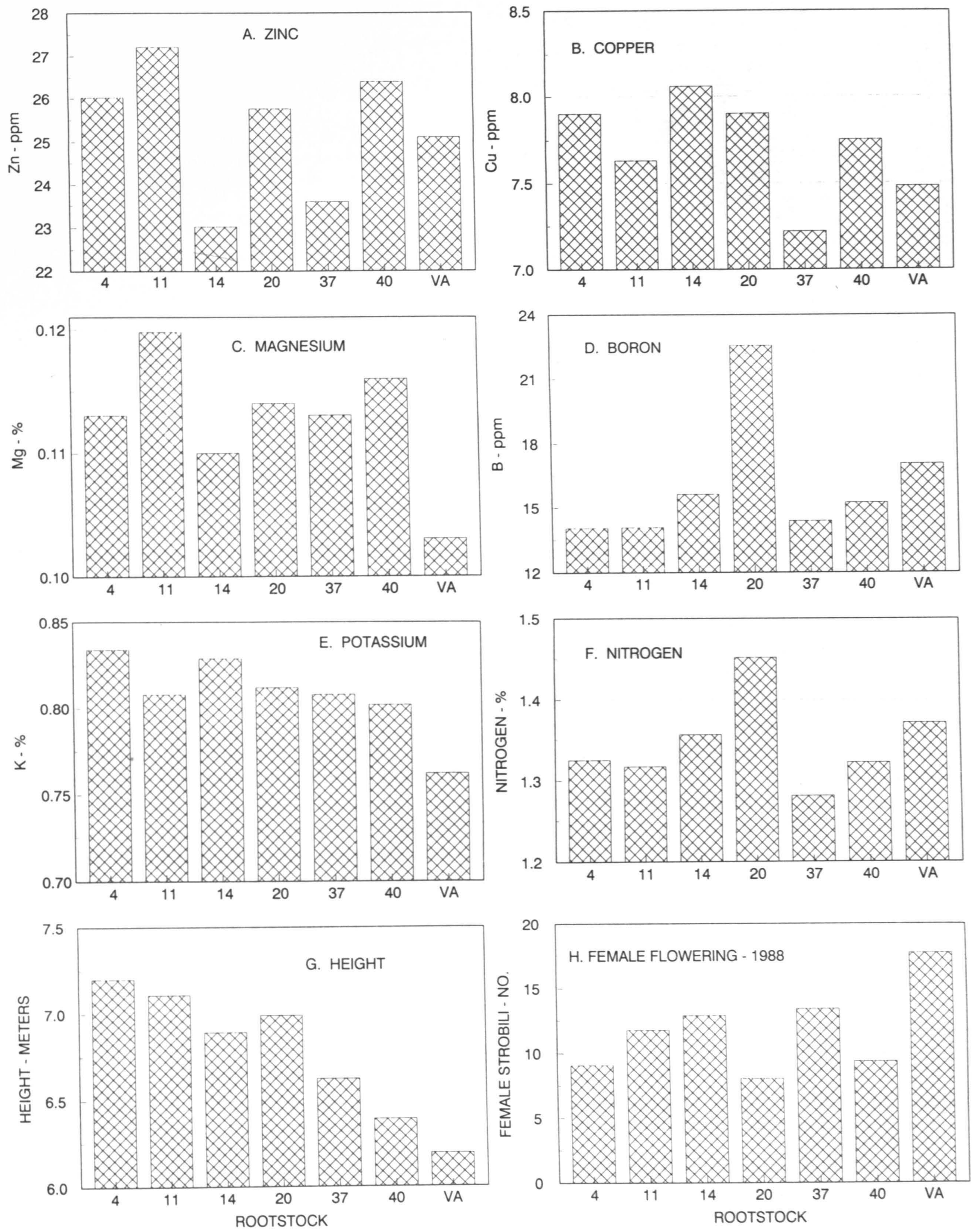


Fig. 5. Mean foliar concentrations by rootstock of several macro- and micronutrients compared to flowering and growth in the Erambert study in 1987.

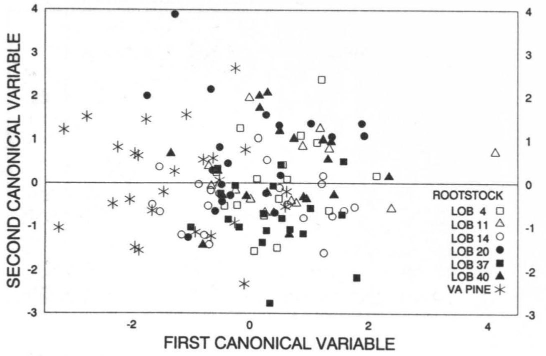


Fig. 6. Scatter plot of the first two canonical variables from the canonical discriminant analysis of rootstock variation in foliar macro- and micronutrients (Erambert study 1987).

4 Conclusions

The importance of scion clone effects on flowering, which has been often observed (Schmidtling 1974), is verified in this study. It is also apparent that variation in foliar nutrients is strongly related to scion clone, a fact that should be taken into account if foliar analysis is to be used as a diagnostic tool.

There is also considerable genetic variation in traits that would be useful for rootstock selection in loblolly pines. The possibility of identifying suitable rootstocks short of actual testing in rootstock trials does not appear to be very promising, however.

The nature of the mechanism behind rootstock effects has not been made any clearer in this experiment. Genetic relatedness between the scion and rootstock does not appear to be an important factor except in enhancing survival of clones with incompatibility problems.

It seems clear that rootstocks do influence mineral uptake, but there was no simple relationship between their effects on mineral uptake and their effects on growth and flowering. The true cause and effect in rootstock-scion relations may lie elsewhere, perhaps with variation in hormones or moisture stress.

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