VARIATION AMONG BLACK SPRUCE CLONES IN NUTRIENT UPTAKE AND EARLY GROWTH AFTER FIELD PLANTING

by

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ABSTRACT

A study was conducted to determine the genetic variation in black spruce (Picea mariana [Mill.] B.S.P) with respect to nutrient uptake and use efficiency on a typical forest soil in central New Brunswick.

The experimental stock originated from ten plus trees that had been selected in 1986 for the establishment of seed orchards. Seedling populations were raised from each plus-tree giving rise to ten half-sib families. From each of these populations ten plants were selected for vegetative reproduction by rooting shoot tips. In this way 98 clonal populations were obtained and field tested in a randomized block design. The plants were remeasured after completion of the first growing season. Since there was significant variation among families and clones at the time of planting, comparisons were made on the basis of annual growth increments and relative growth rates.

Both families and clones varied significantly with respect to height and diameter growth, and gains in component and total plant weights. In all cases, clones contributed more to the total experimental variance than families.

Biomass accretion was closely correlated with N and P uptake (r=0.911 and 0.892, respectively), suggesting that either one or both of the elements were limiting growth factors. Clones superior in growth and nutrient uptake had lower than average shoot:root ratios and, thus, higher than average root biomass. This would have provided the plants of these clones with an enlarged surface for nutrient absorption. Clones superior in growth also ranked highest in N and or P use efficiency, i.e., the amount of biomass produced per unit of element taken up.

Fast-growing plants had accumulated the highest quantities of Al, but the bulk of it was retained in the roots. Aluminum uptake was further correlated with P uptake, suggesting that both elements moved towards the roots as a complex ion.

Key Words: Aluminum, genetic variation, clones, half-sib families, nutrient uptake, nutrient use efficiency, Picea mariana [Mill.] B.S.P.

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INTRODUCTION

The selection of growing stock for reforestation is usually made at the species level. The rationale is that only those species adapted to certain sites should be used (Nambiar 1985). However, there is ample evidence of genetic variation within species with respect to rate of growth at a given site (Owino and Zobel 1977; Morgenstern 1978; Fowler and Park 1982). Such variation has been related in many investigations to the mineral nutrition of the trees (Steinbeck 1966; Brown 1970; Goddard and Hollis 1984).

Investigations into the genetic effects on mineral nutrition have been conducted at the provenance, family and clonal levels. Brown (1970) reported distinct differences among the responses of different provenances of Scots pine (Pinus sylvestris L.) to fertility and moisture treatments. Other workers (Woessner et al. 1975) found differences among and within provenances of loblolly pine (Pinus taeda L.) seedlings in absorption of calcium (Ca) and magnesium (Mg). In the case of phosphorus (P) and potassium (K) uptake, variation existed within, but not among provenances. Similar observations were reported by McClurkin et al. (1971) who also worked with Scots pine.

Variation in nutrient uptake has frequently been found to be greater among families than among provenances. Goddard et al. (1976) reported differential height growth of three- year-old slash

pine (Pinus elliotii Englem.) from selected families to fertilizer treatment on poorly drained, acidic soils. Some families exhibited poor growth on unfertilized soil, but they responded strongly to fertilizer addition. Other families displayed little response to fertilizer treatment and still others exhibited superior growth on both fertilized and unfertilized soils. These observations agree with the views of Jahromi et al. (1976b), namely that the genotype best suited for the site is able to maintain better than average growth under low levels of fertility and, at the same time, is able to respond strongly to increased nutrient availability.

Significant variation at the family level has also been reported for responses to nitrogen (N) treatments. This included the following species: Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) (Bell et al. 1979), American sycamore (Platanus occidentalis L.) (Steinbeck 1971), slash pine (Walker and Hatcher 1965); and tamarack (Larix laricina [Du Roi] K. Koch) (Wanyancha 1986; Wanyancha and Morgenstern 1987a and 1987b).

There are relatively few investigations of mineral responses at the clonal level. Burdon (1971) demonstrated genetic differences among radiata pine (Pinus radiata D. Don) clones whilst growing on soils with low available P. He found that some clones had good height growth despite the low P availability in the soil. In others, growth was satisfactory while in a third group, growth was severely depressed. Differing ability to use P at low concentrations in the rooting medium was also reported by Mason and Pelham (1976) for white birch (Betula papyrifera Marsh.) clones. Not only growth, but also internal nutrient

concentrations may vary at the clonal level. This was shown by Steinbeck (1971) for sycamore clones.

Genotypic variation in response to site has been attributed by some investigators to varying nutrient uptake and use efficiency (Nambiar 1985; Marchner 1986), where nutrient uptake efficiency is given by the amount of a certain element removed per unit volume of rooting medium per unit time, and use efficiency is given by the biomass produced per unit mass of element taken up from the medium (Clark 1983).

The variation among genotypes with respect to mineral nutrition holds certain potential for improved forest production. Where soil fertilization is economically prohibitive and tree growth is dependent on the indigenous fertility of the soil, an advantage might be gained by selecting genotypes with proven nutrient uptake and use efficiency. Alternatively, selection may favour genotypes that have the ability to respond strongly to fertilization. With the prospect for clonal forestry, information at the clonal level appears to be more important today than ever before. During the past two decades, the advantages of clonal selection and improved methods of vegetative reproduction of Norway spruce (Picea abies [L] Karst.) have led to reforestation with clonal stock of that species in Germany and other European countries (Kleinschmit et al. 1977). During the same time methods for vegetative propagation of radiata pine were developed in Australia and New Zealand (Wilcox et al. 1976). Similar methods of planting stock production have been developed for Eucalyptus spp. in Australia

(Hartley 1980), and Sitka spruce (Picea sitchensis [Bong.] Carr.) in Britain (Gill 1983).

Among the species readily reproduced by rooting of shoot cuttings is black spruce (Picea mariana [Mill.] B.S.P.) (Armson et al. 1980). With further refinement of the propagation methods (Phillion 1982a, 1984a, Phillion and Whittiker 1985), a vegetative propagation program by rooting of cuttings has since been developed in Ontario with approximately one million ramets being produced annually at the Northern Clonal Forestry Centre at Moonbeam (Rogers 1989). In Nova Scotia, mass-produced rooted cuttings of black spruce were used for reforestation of land on which forests had been lost to insect pests (Mullin 1990).

Black spruce is an important reforestation species in eastern Canada. Genetic variation in the growth of this species has been documented extensively at the provenance level (Morgenstern 1978; Fowler and Park 1982; Boyle 1985; Boyle and Morgenstern 1986, 1987). Mullin (1985) investigated genotype-nitrogen interaction in full-sib black spruce families by growing plants at three levels of N supply in the greenhouse. He noted significant genetic variation among the families. Maliondo and Krause (1985) found significant effects of soils of varying fertility and a family x soil fertility interaction. They suggested that this was largely due to differences in nutrient uptake ability, particularly uptake of P. Since the soil used in that study was very acidic, it was further suggested that the observed differences in seedling growth also reflected varying degrees of tolerance to high levels of soluble aluminum (Al).

The genetic variation with respect to P uptake and tolerance to Al was further pursued at the clonal level by Cruickshank (1990). This work indicated differential responses of clonal black spruce to phosphate sources of varying Al to P ratio.

So far, most of the research on genotypic variation in black spruce, with respect to mineral nutrition, has been conducted under greenhouse conditions. Such studies are of limited value unless it is known to what extent the results were influenced by the greenhouse environment, and to what extent the response in juvenile stock is correlated with response in older trees. With this in mind, a field experiment was carried out to test 98 black spruce clones. These represent the progenies from 10 open-pollinated superior trees which had been selected earlier for establishment of seed orchards, following the strategy as outlined by Fowler (1986) for the improvement of important tree species in the Maritime Provinces.

The objective of the experiment was to determine the genetic variation among half-sib families and clones of black spruce with respect to growth, nutrient uptake and use efficiency during the first year after planting on a strongly acid soil.

METHODS AND MATERIAL

SEED SOURCE

Seeds were obtained from the New Brunswick Department of Natural Resources and Energy Tree Improvement Unit, at the Kingsclear Nursery, Fredericton N.B. The seeds originated from 10 plus trees, i.e phenotypically superior individuals which had been identified in the Province's tree improvement program (Fowler 1986). The seeds thus represented 10 half-sib families of black spruce, and will henceforth be referred to as families.

The plus trees had been designated as: 01-6, 01-8, 01-36, 01-93, 01-128, 04-7, 04-8, 04-10, 04-40 and 04-42 in the above program. The 01 group had been selected on Crownlands in eastern New Brunswick and 04 group from Crownland and freehold of Fraser Inc. in northwestern New Brunswick. In the present study, the families, given in the same order as above, were redesignated A, B, C, E, F, G, H, I, L and M.

In spring of 1987, populations of seedlings were raised for each family in the University of New Brunswick greenhouse, and 10 plants were selected from each population for vegetative reproduction (Figure 1). The selected seedlings were transplanted into 2-L plastic pots containing a 3:1 peat-vermiculite mixture, and were allowed to

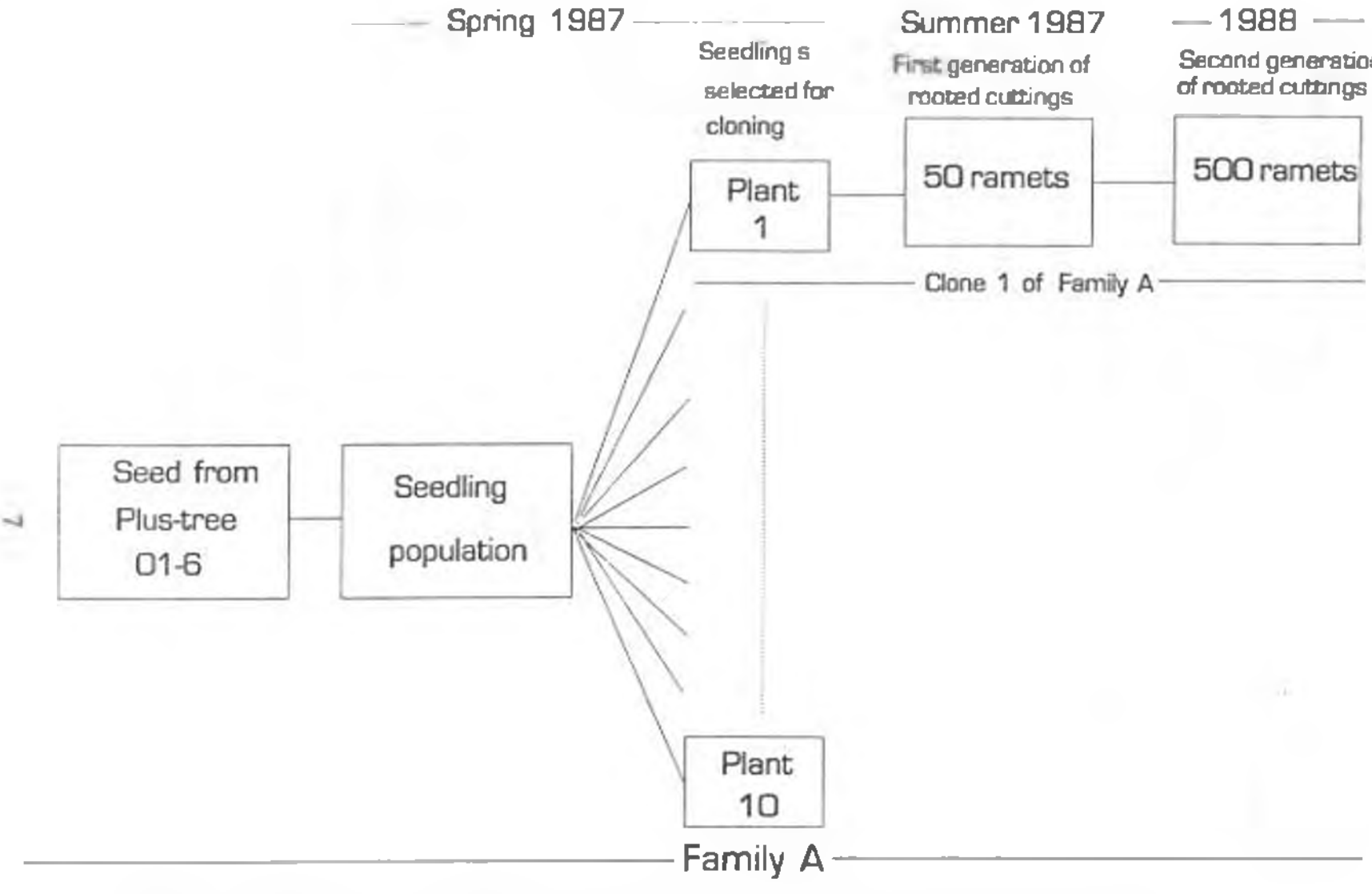

Figure 1. Propagation of clonal experimental stock , using Family A as example

grow to a height of approximately 25 cm. Shoot tips, approximately 5 cm long were clipped, dipped in 0.8 % indole butyric acid and planted into Ferdinand Root Trainers (Carlson 1983) which had been filled with a 3:1 peat-vermiculite mixture. The containers were kept in a mist chamber until rooting occured. This required from 8 to 12 weeks. The rooted cuttings were then transferred to large-cavity (Beaver plastics No. 6) styrofoam containers, which were filled with the same peat-vermiculite mixture, and allowed to grow for an additional 4 months. About 50 rooted cuttings (ramets) were obtained in this way from each seedling (Figure 1).

In the spring of 1988, the first generation of rooted cuttings was transferred to the Kingsclear Nursery, about 10 km west of Fredericton, for further vegetative reproduction. Approximately 10 shoots were taken from each plant to produce a second generation of rooted cuttings. In total, about 500 ramets were produced for each clone and it should be noted that all the trees outplanted were second-stage rooted cuttings (Figure 1).

With a few exceptions (Families B, F and H), rooting occurred readily and survival of the plants in the greenhouse was high. In the fall of 1988, the rooted cuttings were placed outside in a shade frame for overwintering.

Some damage was incurred during overwintering, leading to the loss of Clone 8 and 9 of Family B and a reduction in the number of plants from Clone 1 of Family C, Clones 5 and 6 of Family F and Clone 1 of Family I.

EXPERIMENTAL SITE

The experiment was carried out on Crownland in central New Brunswick, south of Anderson Road, near Five Mile Brook (46° 22'N and 66° 34'W) (Figure 2). The land is licensed to J.D. Irving Ltd. (Fundy License, Block # 407021788). The previous forest, which had been harvested in the spring of 1988, consisted mainly of black spruce and balsam fir (Abies balsamea (L.) Mill.). Also present were white birch (Betula papyrifera Marsh.),trembling aspen (Populus tremuloides Michx.), red maple (Acer rubrum L.), and white pine (Pinus strobus L.).

The area is located about 175 m above sea level. It has a mean annual precipitation of 1200 mm, and mean January and July temperatures of -11°C and 19°C, respectively. The growing season comprises 180 days (Anon. 1980).

SOILS

The area is flat with little or no micro-relief. The soil was classified as an Orthic Humo-Ferric Podzol and it is mapped as a member of the Reece Association (Rees et al. 1991). It has a sandy loam texture and is well to moderately well drained with a remnant forest floor of 2.0 to 5.0 cm. The parent material is a lodgement till, derived from grey sandstone of Pennsylvanian age.

Figure 2. Map of New Brunswick showing the experimental site.

The soil was sampled in October 1988, on a 50 x 50 m grid. Samples were taken from the forest floor and the B and C horizons at 18 points. The soil samples were sieved through a 2-mm sieve and the forest floor samples were screened through a 5-mm steel wire gauze. The samples were then placed in a forced-draft oven and dried at 55° C for 48 hours. Chemical analyses were carried out according to standard laboratory procedure (McKeague 1978). The results are presented in Table 1.

EXPERIMENTAL DESIGN

This study dealt with one component of an experiment which was designed to test families, clones and eight fertility treatments. The latter were obtained by addition of N, P, and Al at two levels and in all possible combinations. The treatment combinations were replicated five times using a randomized block design (Figure 3). Accordingly, each block contained 8 plots. Within each plot, trees of the different clones were planted on randomly chosen rows with 8 seedlings per row. The rows were spaced 1.5 m apart and the trees were planted at 0.5 m distance within the rows. The application of fertilizers was scheduled for the second year after planting. The present study was concerned with growth and nutrient uptake during the first season after planting.

Table 1. Chemical characteristics of the soil from the experiental site.

Horizon	pH (H2O)	Organic C	Total N	Available P	Extract Al	Exchangeable K	Exchangeable Ca	Exchangeable Mg
		%		mg kg-1		c mol kg-1		
FF	3.3	38.0	1.22	44.67	36.15	14.4	20.0	1.48
B	4.4	3.0	0.114	0.21	14.80	0.43	0.28	0.06
C	4.6	0.8	0.042	0.11	7.82	0.34	0.22	0.03

ROAD

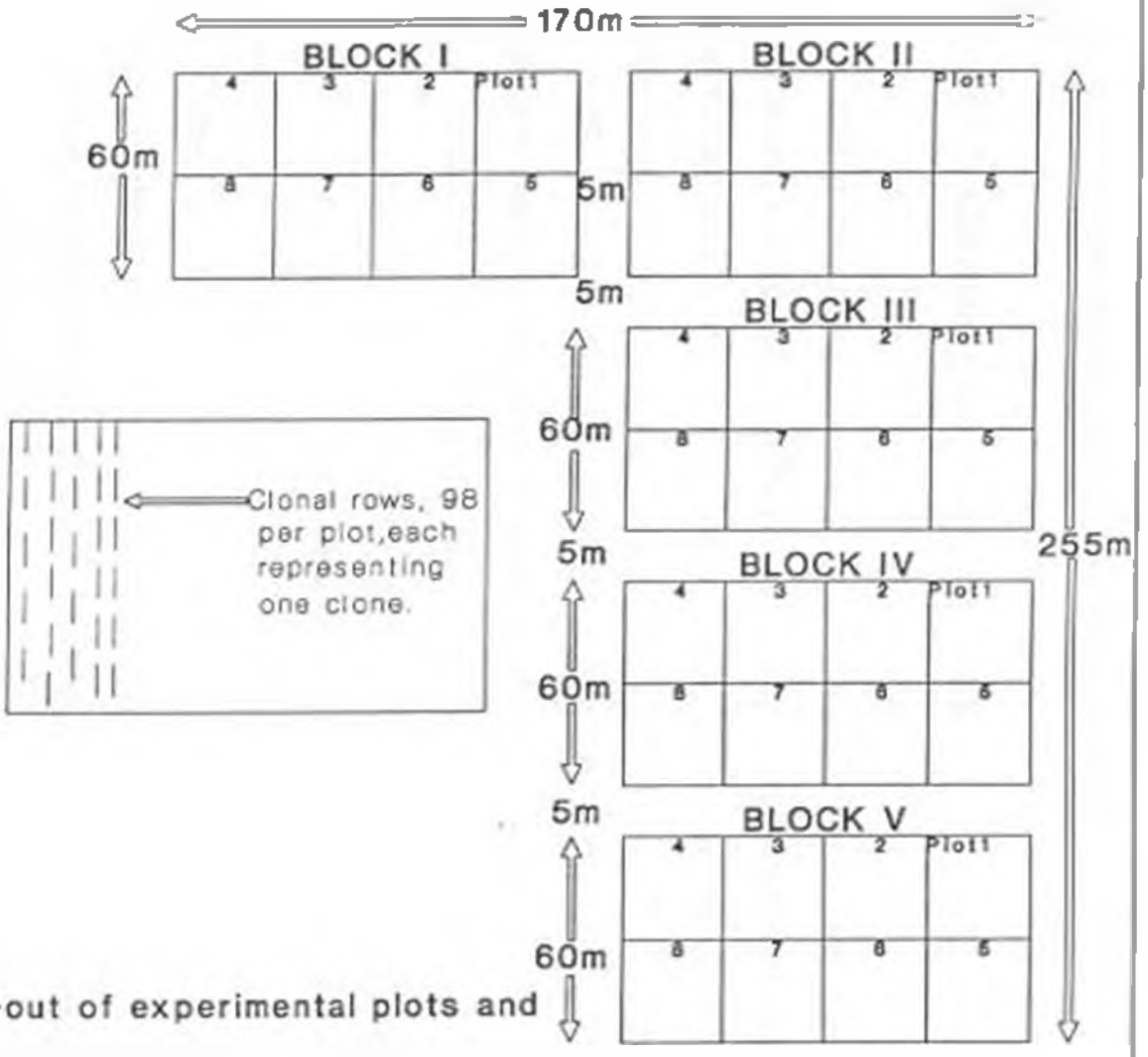

Figure 3. Lay-out of experimental plots and plot 1 enlargement to show rows.

FOREST

Only Blocks II and III were used. These were established early in the season and showed the least variation at initiation of the experiment. The 16 plots in the two blocks were considered replicates for the 10 families and 98 clones (Figure 3).

SITE PREPARATION AND FIELD PLANTING

Site preparation was carried out in the spring of 1989, using barrels and chains. The equipment was moved several times over the land in opposite directions to remove most of the logging slash and to expose mineral soils.

The plants were measured and sorted in the greenhouse before they were taken to the field for planting. Plants required for a row were removed from the original boxes, subjected to root collar and height measurements, tagged and placed in new boxes, identified for a certain plot. One average plant was chosen per clone for destructive sampling and chemical analysis.

The component and total weights of the sampled plants were related to their heights (H) and root collar diameters (RCD) by regression analysis (Hicks 1982). Accordingly, the following equations were developed and subsequently used for estimating the initial weights of all plants taken to the field:

$$\text{Foliage biomass} = 1.1895 + 0.0372(H) + 0.373(RCD).$$

$$r^2 = 0.65 \qquad (1)$$

Stem biomass = 1.436 + 0.0398(H) + 0.4048(RCD).

$r^2 = 0.74$ (2)

Root biomass = 0.7209 + 0.0083(H) + 0.4576(RCD).

$r^2 = 0.45$ (3)

The data for each growth variable were subjected to GLM type II analysis of variance (see page 18) to determine the pre-planting variability.

RESPONSE VARIABLES AND THEIR MEASUREMENTS

Assessment of seedling survival was carried out prior to field sampling in October 1989. The average mortality on all plots was 1% to 3% among all blocks. Occasional animal browsing was observed in some of the plots.

One plant was randomly chosen from each row plot in each plot. In total 1,568 plants were collected for analysis. The plants were carefully removed from the soil with a shovel. Excess soil was shaken off carefully and the sample put into a labelled bag for temporary storage in a cold room.

In the laboratory, soil adhering to the roots was washed off under a stream of tap water and the whole plant was rinsed with distilled water. The shoot lengths of the samples were measured to the nearest mm and their root collar diameters to the nearest 0.1 mm with vernier-type calipers.

The samples were then dissected into shoots and roots and dried in a forced draft oven at 70° C for 72 hours. Needles were separated from stem and branches and dry weights were obtained separately for roots, needles and stem plus branches.

Total plant weights were obtained by adding the component dry weights and growth increments were determined by subtracting the measurements made prior to planting from those of the resampled plants. The plant components were ground in a Wiley mill and analysed for nutrient and Al contents.

CHEMICAL ANALYSIS

The separation of each sample tree into three components created a total of 4,704 sub-samples. This was a larger number than could have been analysed within the time period available. Therefore, composite samples were created by the combination of four plants of the same clone from adjacent plots. In total 1,176 samples were analysed.

Determination of Nitrogen

This element was determined by the Kjeldahl method of Bremner and Mulvaney (1982), modified for use with semi-automatic equipment (Buchi/Brinkmann Kjeldhal nitrogen system). Sub-samples of the ground tissue (90-100 mg) were digested with 5.0 ml of concentrated H_2SO_4 to which had been added 3.0 g of digestion mixture. This mixture contained Se, $CUSO_4.5H_2O$ and K_2SO_4 in

ratios of 1:10:100. Nitrogen in the digest was determined by steam distillation. Ammonia released during the distillation was collected in 2% Boric acid at pH 5.5. The boric acid was back-titrated with 0.04 N H_2SO_4.

Determination of Phosphorus, Potassium, Calcium, Magnesium and Aluminum

Sub-samples, weighing 400 mg - 500 mg, were dry-ashed in Coors porcelain crucibles following, with minor modifications, the method by Allen and Parkinson (1969). The crucibles were placed in a cold muffle furnace. Temperature was allowed to rise gradually to 450° C, and to remain at this level for two hours. Crucibles were then removed from the furnace and allowed to cool in a desiccator. The ash residue in the crucible was moistened with distilled water and 5 ml of 8 M HCl were added to it. Crucibles were then placed in a 95° C water bath and kept there for 30 minutes. Contents of the crucibles were filtered through Whatman #44 filter paper and the filtrates were diluted to 50 ml.

Phosphorus was determined in the filtrate by an auto-analyser (TRAACS 8000), using the molybdo-vanadate reagent (Technicon Industrial Method number 792-86 T). Contents of K, Ca, Mg and Al were determined by atomic absorption spectrophotometry (Price 1979). For determination of the first three elements, a 2-ml aliquot of the extract was transfered to a 20 ml test tube. Two ml of 1.5% $LaCl_3$ solution and 1 ml of 1 N HCl were added and contents of the tube

were made up to 20 ml volume with deionized water. Measurements were made by a Varian atomic absorption spectrophotometer Model 2000.

Aluminum contents of the roots were determined by the same unit, using a nitrous oxide - acetylene flame. Test solutions were prepared with addition of KCl as an ionization depressant. Aluminum concentrations of the foliage, stems and branches were determined by a Varian Model GTA-96 graphite furnace (Price 1979).

STATISTICAL ANALYSIS

The data were evaluated by a SAS General linear model (GLM) technique for unbalanced analysis of variance (ANOVA) (Freund and Littel 1981). Plot and family and clones were considered as random factors. Main effects and first order interactions were determined by application of the following ANOVA type II model (Zar 1984) :

$Yijkn = U + Pi + Fj + Ck(j) + En(ijkn)$.

Where $Yijkn$ is the n^{th} observation in the i^{th} plot of the k^{th} clone within j^{th} family.

U is the experimental mean.

Pi is the effect of i^{th} plot (i=1,2,3,.....16).

Fj is the effect of j^{th} family (j=1,2,3.....10).

Ck(j) is the effect of k^{th} clone within family j

(k=1,2,3,.....10).

En(ijkn) is the random error associated with the n^{th} replicate of combination i,j and k (n=1).

F-ratios were determined by division of the Plot, Family and Clone mean squares (M.S.), by the error mean square (E.M.S.), Clone M.S., and E.M.S., respectively.

A simplified ANOVA (Ycd = U + Fc + Ecd) was used to test family means of nutrient contents prior to planting.

RESULTS

DIFFERENTIAL GROWTH DURING THE REARING STAGE

Although the plants used in this study had been raised under the same conditions, they varied widely in size at the time of planting. Analysis of variance (Table 2) indicated significant differences among families and clones for nearly all response variables.

Certain families were easier to reproduce vegetatively than others, i.e. the cuttings from plants of one family rooted faster than cuttings from plants of other families. Such differences were also noted to exist among plants of the same family. With the advantage of an early start, the fast-rooting cuttings developed into the tallest and strongest plants by the time of field planting. It is also possible that these plants had a higher relative growth rate than the plants from the more slowly rooting cuttings.

According to Table 3 and Figure 4, Families A and E were most advanced in growth and plants of Families B and I ranked lowest with respect to height, root collar diameter, and dry weights. Family M occupied an intermediate position. Variation within families was as large or larger than variation among families (Figure 5).

Table 2. Comparison of families and clones after selection for planting (results of ANOVA)

Source of Variation	Degrees of Freedom	Shoot Height	Root Collar Diameter	Root Weight	Stem Weight	Foliage Weight	Total Biomass	Shoot Root Ratio
		F-Ratio						
Plot	15	85.31***	63.63***	80.37***	105.62***	105.69***	102.3***	54.3***
Family	9	4.39***	1.85n.s	2.14**	3.43***	3.44***	3.12***	4.31***
Clone (Family)	88	23.05***	6.60***	8.42***	15.69***	15.78***	13.57***	18.13***
E.M.S.	1376							

Significance Levels: ***, 0.1%; **, 1.0%; *, 5.0%; n.s., not significant

Table 3. Ranking of families (A-M) according to growth before field planting (Duncans Multiple Range Test,n=10).

Growth Parameter	Rank 1	2	3	4	5	6	7	8	9	10
Height Growth	A	L	E	C	M	G	B	F	H	I
Root Collar Diameter	E	H	A	I	C	L	G	M	F	B
Root Weight	E	A	H	L	C	I	G	M	F	B
Stem Weight	A	E	L	C	M	G	H	F	B	I
Foliage Weight	A	E	L	C	M	G	H	F	B	I
Total Weight	A	E	L	C	M	H	G	F	I	B
Shoot:Root Ratio	A	L	E	C	M	G	F	B	H	I

Families ranked in descending order

Families underscored by the same line are not significantly different at 5% level

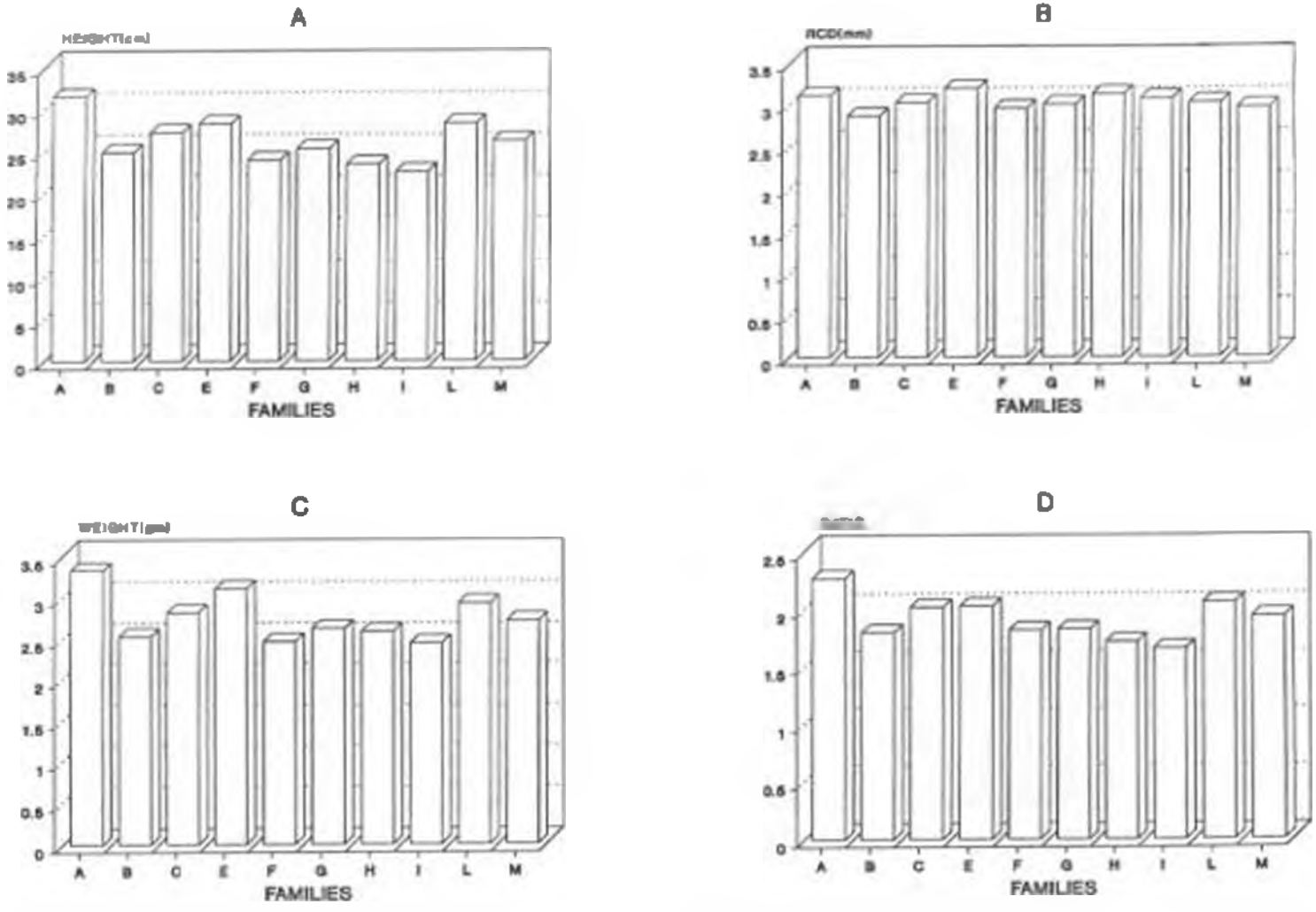

Figure 4. Among-family comparison prior to planting: A, heights; B, root collar diameters; C, total weights; D, shoot:root ratios (n=10).

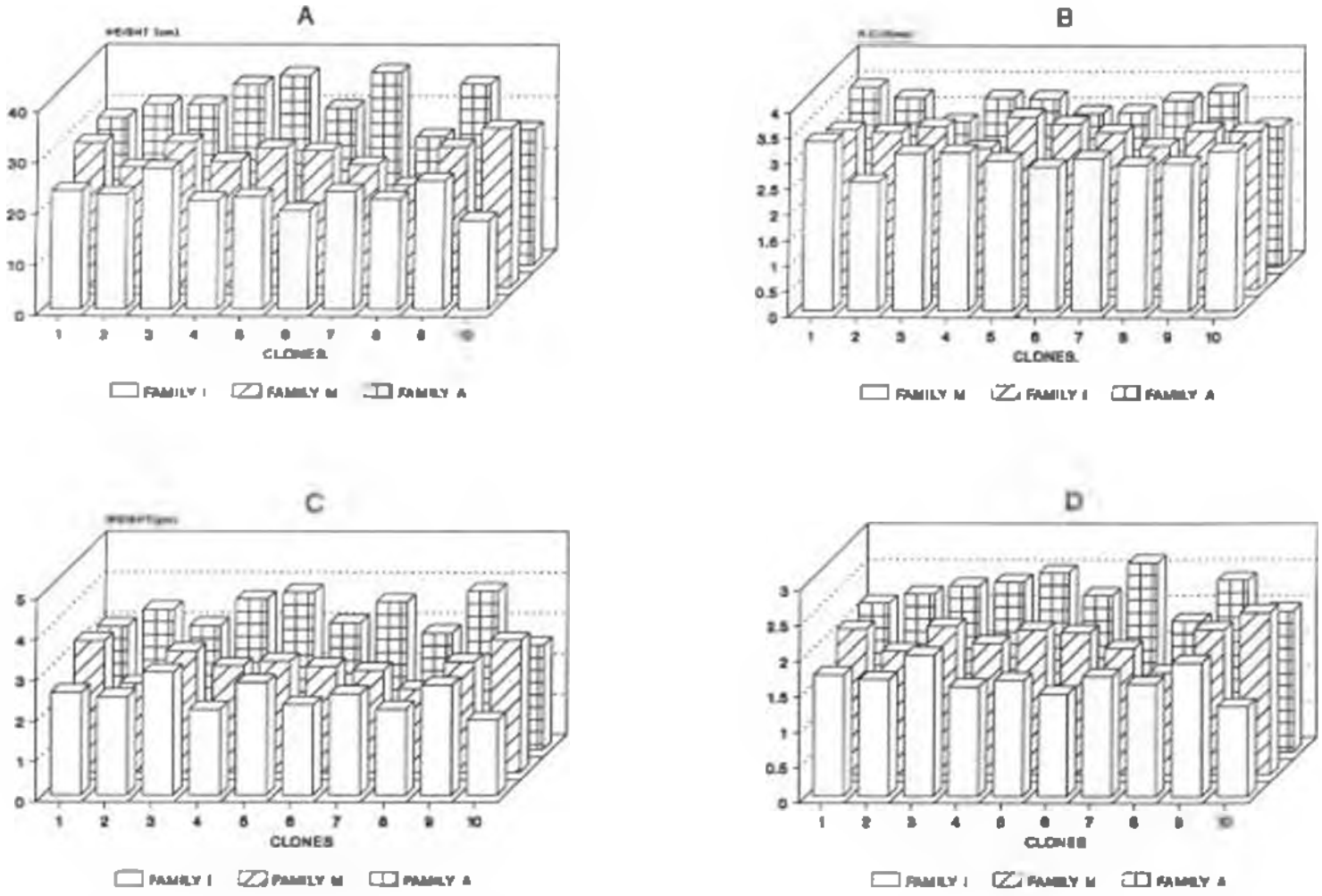

Figure 5. Among clones comparison prior to planting: A, heights; B, root collar diameters; C, total weights; D, shoot:root ratios (n=10).

PREPLANTING NUTRIENT CONTENTS

There was also wide variation among families with respect to nutrient contents prior to planting. Families A, C and E were characterised by low N concentrations (Table 4). Highest N concentrations were shown by Families H and M. Phosphorus ranged from 0.14% to 0.21%, with families C and E showing the lowest concentrations and Family H the highest concentration. Family M also distinguished itself by above average K, Ca, and Mg concentrations.

According to foliar nutrient standards from the literature (Morrison 1974) N concentrations ranged from critical to deficient, and P from critical to adequate. Concentrations of K, Ca and Mg were in the sufficiency range for all the families (Appendix 1). Aluminum concentrations, although varying significantly with family, reflected values that are commonly reported in the literature for conifer foliage (Mallondo 1986).

The element contents, per plant (Table 5), generally reflected the size of the plants and, in the case of N and P, more closely the weight of foliage than the total weight of the plants. However, according to Duncan's Multiple Range test, there were no significant differences among families in nutrient content except in the case of K (Table 6).

Plants of Families E, A and L were ranked the highest with respect to K content and Families F and I lowest (Tables 5 and 6).

Table 4. Mean foliar element concentrations of families prior to planting (n = 10).

Family	N	P	K	Ca	Mg	AL ppm
	g/kg					mg/kg
A	8.50	1.50	6.70	5.30	1.20	33.00
B	11.20	1.60	7.00	6.50	1.30	24.00
C	8.90	1.40	6.90	5.50	1.10	24.00
E	8.90	1.40	6.40	5.50	1.00	23.00
F	12.40	1.60	6.60	7.00	1.30	32.00
G	12.80	1.70	7.10	5.60	1.10	43.00
H	15.00	2.10	7.00	7.60	1.40	40.00
I	14.00	1.90	6.60	8.50	1.70	43.00
L	11.40	1.70	7.80	6.20	1.40	29.00
M	14.90	1.80	8.10	8.90	1.60	34.00
AVG.	11.80	1.70	7.00	6.70	1.30	32.50

Table 5. Mean nutrient and Al contents of plants representing Families A - M prior to planting (n = 10).

Family	N	P	K	Ca	Mg	Al
	mg/plants					
A	22.59	3.89	17.94	14.07	6.61	1.27
B	18.86	3.08	14.83	12.00	6.17	0.77
C	19.04	3.10	15.13	11.49	4.77	0.65
E	21.77	3.62	18.03	13.96	7.29	1.28
F	20.79	3.27	13.91	12.70	6.64	1.24
G	23.17	3.67	15.93	11.83	6.35	0.95
H	24.79	3.95	15.25	12.77	5.17	0.79
I	23.37	3.63	13.52	14.76	6.69	1.06
L	22.77	3.83	17.61	13.21	5.98	0.93
M	23.03	3.84	16.02	15.09	5.02	0.76
AVG.	22.02	3.59	15.82	13.19	6.07	0.97

Table 6. Ranking of Families (A - M) according to nutrient and Al contents (mg/plant) prior to field planting (Duncan's Multiple Range test n = 10).

Nutrient	Rank									
	1	2	3	4	5	6	7	8	9	10
Nitrogen	H	I	G	M	L	A	E	F	C	B
Phosphorus	H	A	M	L	G	I	E	F	C	B
Potassium	E	A	L	M	G	H	C	B	F	I
Calcium	M	I	A	E	L	H	F	B	G	C
Magnesium	E	I	F	A	G	B	L	H	M	C
Aluminum	E	A	F	I	G	L	H	B	M	C

Families ranked in descending order

Families underscored by the same line are not significantly different at 5% level

Root biomass may have been affected by the availability of potassium. For example Families E and A, which had the highest K contents (Table 6), also had the largest root biomass (Table 3). Furthermore, K contents were closely correlated with all growth variables monitored (Table 7). This suggests that plant development may have been constrained by shortages of K supply during part or all of the rearing stage.

FIELD GROWTH

Growth of plants during the first season after planting was determined by remeasurement of the same variables included in the preplanting assessments. Comparison of preplanting and field measurement is made in Figure 6. Depending on family, shoot height increased by 30 to 40 %, root collar diameter by 110 to 130 % and total plant weights by 300 to 500 %, respectively. Except in Family A, shoot:root ratios remained about the same or increased only slightly during field growth.

Increments in height and root collar diameter, and accretions in plant total and component dry weights are shown in Table 8. These data show variation not only among families but also among clones within families for the various morphological traits.

Table 7. Matrix of Pearson correlation coefficients between clonal nutrient contents (mg/plant) and morphological traits prior to planting.

Morphological Traits	N	P	K	Ca	Mg
			Prior to Planting		
Height	0.493 ***	0.593 ***	0.808 ***	0.577 ***	0.314 ***
Root Collar Diameter	0.651 ***	0.687 ***	0.740 ***	0.665 ***	0.362 ***
Root Weight	0.651 ***	0.728 ***	0.830 ***	0.708 ***	0.382 ***
Stem Weight	0.605 ***	0.702 ***	0.878 ***	0.683 ***	0.370 ***
Foliage Weight	0.605 ***	0.701 ***	0.878 ***	0.683 ***	0.369 ***
Total Biomass	0.624 ***	0.718 ***	0.880 ***	0.699 ***	0.378 ***

Significance Levels: ***, 0.1%; **, 1.0%; *, 5.0%; n.s., not significant (d.f. 90)

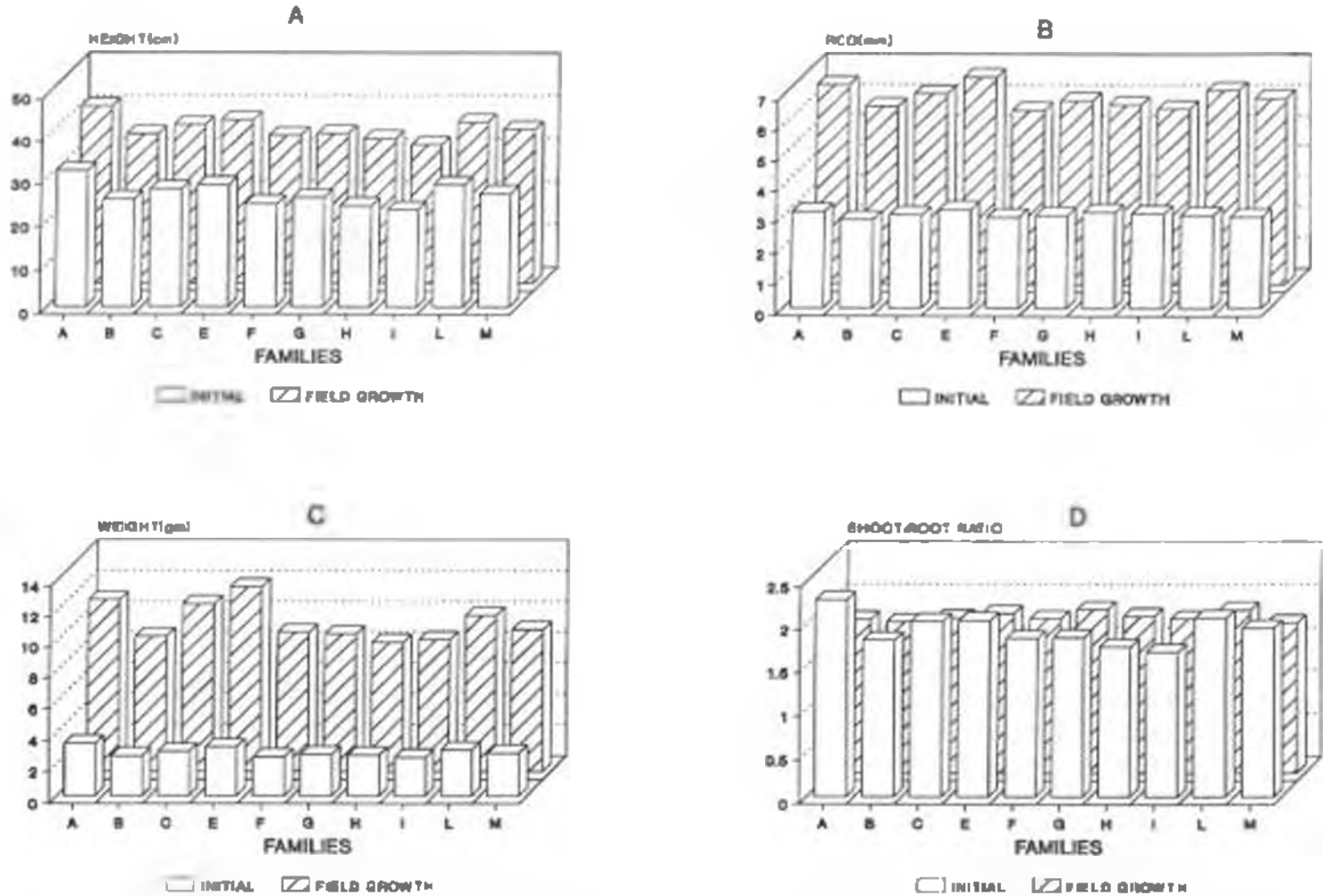

Figure 6. Comparison of plant sizes at initiation of the experiment and after completion of the first field season: A, heights; B, root collar diameters; C, total weights and D, shoot:ratios of Families A to M. (n=10).

Table 8. Mean plant growth during the first field season by family and clone (n = 16).

Clone	Family A	B	C	E	F	G	H	I	L	M
					Height Increment(cm)					
1	10.31	9.00	8.90	9.81	9.00	9.69	11.00	8.87	9.50	10.94
2	9.18	7.56	10.07	9.44	10.12	9.69	10.50	8.87	12.00	7.00
3	10.31	10.56	10.31	10.75	10.37	11.87	8.56	9.50	8.69	9.87
4	8.37	10.31	9.18	10.87	9.69	11.44	12.94	12.19	9.75	7.81
5	8.94	7.81	11.50	9.81	9.45	10.31	12.87	8.12	7.37	10.87
6	10.31	7.78	7.87	8.75	12.50	8.37	8.75	10.12	9.81	10.94
7	9.62	9.31	12.19	10.37	12.06	10.37	10.13	8.31	9.75	9.62
8	8.44	-	9.00	9.12	11.13	9.75	8.00	8.80	8.18	10.12
9	8.75	-	9.69	11.19	14.00	8.50	10.94	11.06	8.81	13.12
10	10.00	8.28	9.75	9.40	9.57	8.00	10.50	11.45	9.67	8.62
Mean	9.43	8.85	9.88	9.95	10.36	9.80	10.36	9.69	9.34	10.03
					Root Collar Diameter Increment (mm)					
1	3.69	2.72	2.75	3.31	3.19	3.25	4.10	2.61	3.63	3.37
2	4.24	2.16	4.03	3.28	2.43	3.69	3.05	2.61	2.84	2.77
3	3.12	3.54	3.71	3.33	2.41	3.00	2.20	2.83	3.52	3.82
4	3.55	2.63	2.66	4.34	2.23	2.58	3.05	2.70	3.31	2.89
5	3.28	3.29	2.64	3.99	2.53	2.37	2.51	2.57	3.06	2.95
6	2.81	2.18	3.57	3.86	3.12	2.59	2.77	3.18	3.37	2.91
7	2.88	3.33	3.13	3.89	2.72	3.66	2.79	2.45	3.45	3.26
8	3.38	-	3.24	3.21	3.48	3.02	2.15	2.95	3.45	2.68
9	3.95	-	3.82	3.38	2.50	3.43	2.72	2.46	3.52	2.87
10	3.15	2.79	2.55	3.37	2.79	2.46	2.26	2.31	3.40	3.66
Mean	3.41	2.84	3.22	3.59	2.73	3.00	2.64	2.70	3.34	3.13

Table 8 (Continued)

Clone	Family A	B	C	E	F	G	H	I	L	M
					Root Weight Accretion (gm)					
1	3.24	2.51	2.35	2.92	3.09	1.64	2.05	2.96	2.79	3.15
2	3.39	1.95	3.99	3.69	2.44	2.45	2.13	2.57	2.33	1.31
3	2.91	2.78	3.39	3.48	3.23	2.07	1.84	2.32	2.42	2.72
4	3.02	1.62	2.85	3.68	2.29	2.29	2.10	2.03	2.57	2.87
5	3.87	2.44	2.29	3.13	1.95	1.41	2.53	2.01	2.56	2.46
6	2.31	1.22	2.41	4.34	1.60	2.91	2.47	3.16	2.87	2.57
7	3.08	2.97	2.79	3.62	2.03	3.22	2.58	2.21	2.34	2.66
8	3.46	-	3.61	2.76	2.32	2.11	1.57	2.11	2.80	2.28
9	4.09	-	4.02	2.52	4.01	2.81	1.78	2.23	3.50	2.67
10	2.39	3.26	3.34	3.57	2.53	1.94	2.42	1.48	3.01	3.20
Mean	3.17	2.35	3.13	3.37	2.49	2.29	2.15	2.35	2.71	2.65
					Stem Weight Accretion (gm)					
1	3.05	2.21	2.22	3.16	2.70	2.46	3.57	2.35	3.62	3.33
2	4.38	1.58	4.13	3.17	1.89	3.31	3.37	2.45	3.24	1.73
3	3.28	3.38	4.15	3.48	2.65	2.73	1.99	2.74	3.33	2.85
4	3.50	1.92	2.48	4.60	1.88	2.31	2.86	2.35	3.42	2.73
5	3.86	2.78	2.71	3.87	2.59	2.20	2.50	2.06	2.78	2.72
6	2.57	1.61	3.37	4.20	2.71	3.04	2.35	2.90	3.20	2.43
7	2.48	2.88	3.54	4.16	2.46	3.77	2.93	2.42	2.14	2.72
8	2.98	-	3.49	2.99	2.94	2.63	2.03	2.17	3.09	2.26
9	4.10	-	4.02	3.42	2.51	3.78	2.48	2.59	3.24	2.52
10	2.93	2.56	2.44	3.29	2.38	1.97	2.28	2.18	3.60	3.25
Mean	3.32	2.37	3.29	3.64	2.44	2.82	2.56	2.45	3.15	2.69

Table 8 (Continued)

Clone	A	B	C
1	1.18	1.28	1.34
2	1.82	1.44	1.96
3	1.90	1.41	2.18
4	1.46	1.22	1.51
5	1.36	1.65	1.46
6	1.14	0.71	1.31
7	0.91	1.63	2.00
8	1.44	-	1.80
9	1.63	-	2.21
10	1.53	1.31	2.11
Mean	1.44	1.34	1.81
1	7.47	5.99	5.92
2	9.59	4.98	10.07
3	8.10	7.57	9.73
4	7.98	4.76	6.84
5	9.08	6.87	6.46
6	6.02	3.53	7.10
7	6.46	7.47	8.33
8	7.89	-	8.91
9	9.82	-	10.24
10	6.86	7.13	7.89
Mean	7.93	6.06	8.22

Family						
E	F	G	H	I	L	M
Foliage Weight Accretion (gm)						
1.81	1.84	0.72	1.06	1.63	0.85	1.54
2.26	1.35	1.37	0.91	1.79	1.66	0.83
1.96	1.84	1.46	0.96	1.39	1.28	1.63
2.45	1.28	1.15	1.20	1.26	1.19	1.39
1.96	1.77	0.81	1.36	1.21	1.13	1.18
2.01	1.60	1.72	1.16	1.83	1.91	1.55
2.64	1.53	1.76	1.16	1.34	1.02	1.74
1.24	1.38	1.37	0.59	1.34	1.71	1.46
1.42	2.47	1.27	0.81	1.34	1.62	1.20
1.97	1.39	1.00	1.41	1.12	1.71	1.55
1.97	1.56	1.26	1.05	1.43	1.41	1.42
Total Plant Weight Accretion (gm)						
7.88	7.63	4.82	6.69	6.95	7.26	8.02
9.11	5.67	7.13	6.41	6.82	7.23	3.88
8.91	7.72	6.26	4.79	6.45	7.03	7.20
10.74	5.46	5.77	6.16	5.64	7.19	6.98
8.97	6.31	4.42	6.39	5.28	6.48	6.37
10.54	5.91	7.67	5.98	7.89	7.98	6.56
10.41	6.02	8.76	6.66	5.96	5.50	7.13
6.98	6.65	6.12	4.19	5.62	7.60	6.00
7.36	8.99	7.86	5.09	6.16	8.35	6.39
8.84	6.30	4.92	6.11	4.78	8.32	7.99
8.97	6.49	6.37	5.76	6.23	7.28	6.78

Table 8 (Continued)

Clone	Family									
	A	B	C	E	F	G	H	I	L	M
	Shoot:Root Ratio of Total Plant									
1	1.39	1.53	1.66	1.93	1.56	2.08	2.64	1.46	1.75	1.55
2	1.89	1.68	1.57	1.55	1.30	2.02	2.08	1.95	2.22	2.09
3	1.88	1.81	1.87	1.64	1.51	2.11	1.84	1.84	2.17	1.70
4	1.69	2.60	1.55	2.08	1.57	1.59	2.17	1.94	1.89	1.62
5	1.44	1.89	1.96	2.03	3.39	2.84	1.60	2.28	1.58	1.77
6	1.94	2.01	2.24	1.47	2.62	1.72	1.49	1.59	2.05	1.56
7	1.15	1.64	2.07	2.02	2.20	1.92	1.76	1.70	1.59	1.71
8	1.46	-	1.57	1.70	1.91	1.99	1.75	1.78	1.78	1.71
9	1.51	-	1.66	1.96	1.24	2.05	1.96	1.80	1.42	1.53
10	2.41	1.23	1.56	1.57	1.71	1.68	1.93	3.33	2.00	1.51
Mean	1.67	1.80	1.76	1.79	1.86	2.00	1.85	1.92	1.85	1.66

Family Effects

Gains in root collar diameter, total and component plant weights varied significantly with family but height growth and shoot:root ratio did not (Table 9). The contribution to the total variance ranged from about 6 % to 12 %, depending on the response variable (Table 10). According to the multiple-range test, Family E ranked highest for root collar diameter and all weight measurements (Table 11). This family ranked also near the top in the pre-planting assessment. The lowest gains were shown by families H and B.

Clonal Effects

All morphological traits varied significantly among clones within families (Table 9). According to Table 10, clones constituted a greater source of variation than families for all response variables.

Based on diameter growth and weight increments, Clone 4 of Family E was the best performer of the total clonal population tested. Clones 6 and 7 of the same family showed the highest gains in root and foliage weight, respectively. With the somewhat lower than average height growth and stronger than average root collar diameters, the clones of Family E included the sturdiest plants sampled. In contrast, some of the clones in Families I, H and M, with lower than average diameter growth and greater than average height

Table 9. Analysis of variance of increments in all response variables during the first growing season.

Source of Variation	Degrees of Freedom	Shoot Height	Root Collar Diameter	Root Weight	Stem Weight	Foliage Weight	Total Weight	Shoot Root Ratio
		F-Ratio						
Plot	15	4.51***	54.61***	10.18***	30.68***	13.21***	17.29***	13.87***
Family	9	1.08n.s.	4.28***	5.75***	5.36***	6.41***	6.82***	0.82n.s.
Clone (Family)	90	1.77***	3.48***	3.44***	4.59***	3.43***	3.81***	3.06***
E.M.S.	1368							

Significance Levels: ***, 0.1%; **, 1.0%; *, 5.0%; n.s., not significant

Table 10. Absolute variance components (V.C.) and percent of total variance (%) for height and root collar diameter increments and dry weight accretions. (Computations based on expected mean square.)

Variance Components	Height Growth		Root Collar Diameter		Root Weight		Stem Weight		Foliage Weight		Total Biomass		Shoot:Root Ratio	
	V.C.	V.C%	V.C.	V.C%	V.C.	V.C%	V.C.	V.C%	V.C.	V.C%	V.C.	V.C%	V.C.	V.C%
Plot	0.653	4.27	0.443	30.28	0.119	7.24	0.295	18.15	0.056	9.08	0.959	11.29	0.083	11.09
Family	0.049	0.00	0.092	6.29	0.157	9.55	0.169	10.40	0.059	9.56	0.999	11.76	0.001	0.00
Clone (Family)	0.922	6.02	0.129	8.82	0.194	11.80	0.227	13.97	0.071	11.51	1.046	12.31	0.082	10.96
Error	13.724	89.71	0.799	54.61	1.174	71.41	0.934	57.48	0.431	69.85	5.493	64.64	0.583	77.95
Total	15.299	100.00	1.463	100.00	1.644	100.00	1.625	100.00	0.617	100.00	8.497	100.00	0.748	100.00

Table 11. Ranking of families (A-M) according to field performance (Duncans Multiple Range Test)

Growth Parameter	Rank 1	2	3	4	5	6	7	8	9	10
Height Growth	H	F	M	E	C	G	I	A	L	B
Root Collar Diameter	E	A	L	C	M	G	B	F	I	H
Root Weight	E	A	C	L	M	F	B	I	G	H
Stem Weight	E	A	C	L	G	M	H	I	F	B
Foliage Weight	E	C	F	A	M	I	L	B	G	H
Total Weight	E	C	A	L	M	F	G	I	B	H
Shoot:Root Ratio	G	I	F	H	L	B	E	C	A	M

Families ranked in descending order

Families underscored by the same line are not significantly different at 5% Level

growth, contained the least sturdy plants. Clonal variation in height growth was particularly strong in Family M, with the smallest and tallest trees differing nearly by a factor of 2. Family H included the clones with the lowest foliage and lowest total plant biomass (Table 8).

According to Table 12, there were low but significant correlations between growth variables measured before and after one growing season. Height increments were negatively correlated with all original growth variables except root collar diameter (Table 12).

The gain in total weight of the plants increased with increasing pre-planting measurements of all growth variables. The closest correlations were observed between gain in root weight and preplanting foliage, and between stem weight and total plant weight.

Further comparison is made of selected clones in Figure 7. Although Clone 4 of Family E was smaller than Clone 9 of Family M at the time of planting, it grew at a faster rate in the field than the Family M clone so that it ranked higher in weight after the completion of the growing season than the latter. Similar relationships were observed for Clones M9 and M2 and also B2 and M2.

The differential response among clones may suggest variable rates of adaptation to the field environment and may further explain the low degree of correlation between pre and post-planting measurements.

Table 12. Pearson correlation coefficients between clonal growth variables measured prior to planting and after one growing season.

	Height2	Root Collar Diameter2	Root Weight2	Stem Weight2	Foliage Weight2	Total Weight2
Height1	-0.253 ***	0.165 ***	0.503 ***	0.335 ***	0.051 n.s.	0.381 ***
Root Collar Diameter1	-0.094 n.s.	-0.092 n.s.	0.395 ***	0.181 ***	0.065 n.s.	0.268 ***
Root Weight1	-0.151 **	-0.026 n.s.	0.475 ***	0.247 ***	0.076 n.s.	0.335 ***
Stem Weight1	-0.221 ***	0.085 n.s.	0.525 ***	0.317 ***	0.066 n.s.	0.386 ***
Foliage Weight1	-0.222 ***	0.086 n.s.	0.526 ***	0.319 ***	0.066 n.s.	0.387 ***
Total Weight1	-0.208 ***	0.062 n.s.	0.522 ***	0.306 ***	0.069 n.s.	0.381 ***

Significance Levels: ***, 0.1%; **, 1.0%, *, 5.0%; n.s., not significant (d.f. = 90)
Variable followed by 1 represents traits prior to planting
Variable followed by 2 represents traits after planting

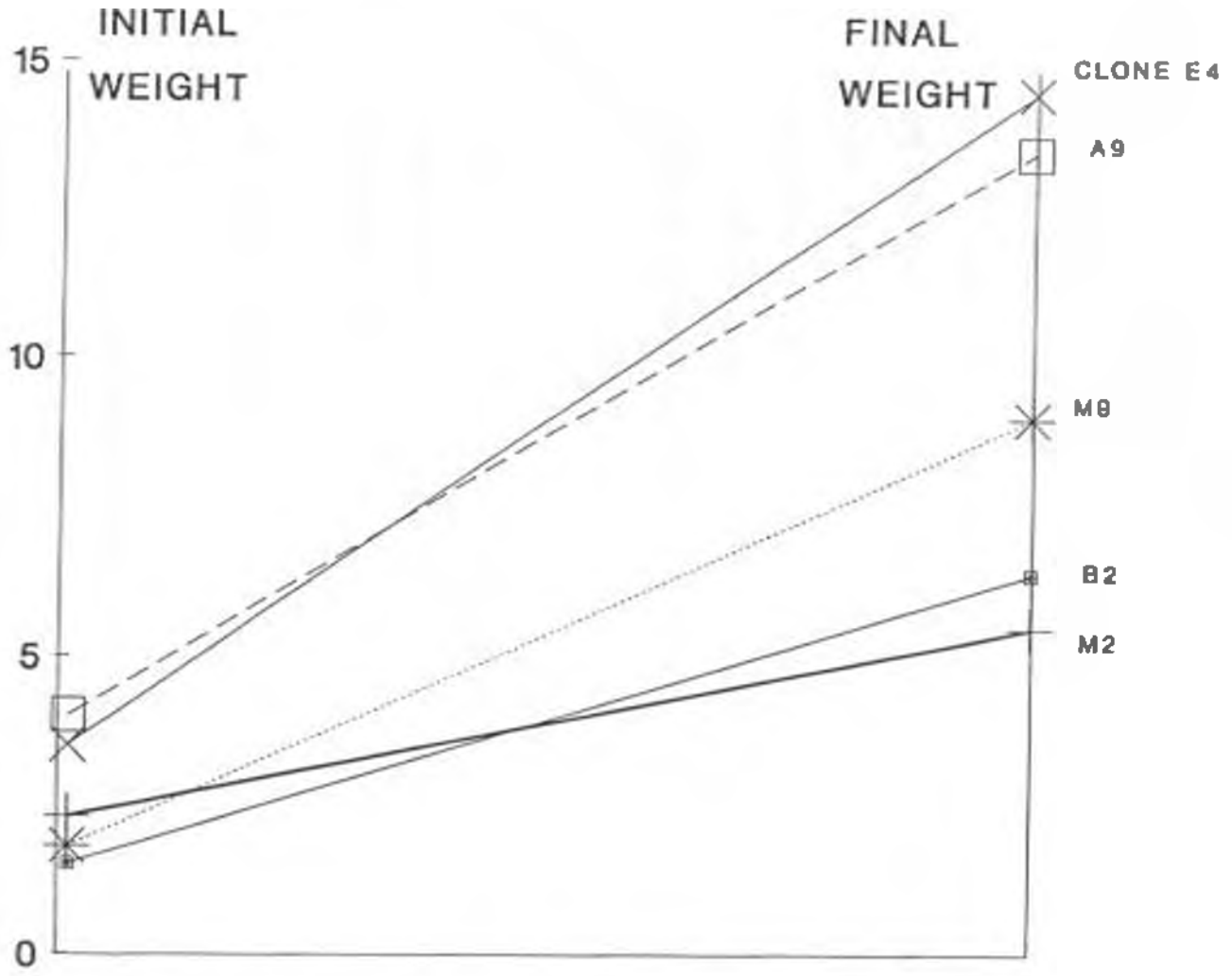

Figure 7. Growth increment of selected clones during the first field season.

Plot Effects

The analysis of variance also revealed a significant plot effect (Table 9). This source contributed from 4 % to 30 % to the total variance, depending on the growth variable. Judging from plant performance, Plot 6 in Block III provided the best conditions for growth (Table 13).

The plot effect indicates strong spatial variability of soils in the experimental site. An important factor is assumed to be the forest floor, which was removed in large part from some portions of the experimental area.

Weight accretions in roots were positively correlated with pre-planting nutrient contents, particularly the contents of K (Table 14). Positive correlations were also found for pre-planting K contents and accretion in stem and total plant weights. In contrast, gains in foliage weight were negatively correlated with pre-planting N content, and height growth was negatively correlated with the pre-planting contents of all nutrients.

RELATIVE GROWTH

Height and root collar diameter growth, and weight gains during the field season are given as percent of the respective original conditions (Table 15). Accordingly, the mean relative height increments ranged from 24 - 48%; root collar diameter increments

Table 13. Ranking of plots (III/1 - III/8) according to growth performance (results of Duncans Multiple Range Test).

Growth Parameter	Rank 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Height	III/6	II/3	III/7	III/4	II/5	II/7	III/4	III/8	III/3	III/5	II/4	II/6	II/8	II/2	II/1	III/1
Root Collar Diameter	III/6	II/7	III/2	III/5	III/3	III/4	III/1	II/6	III/7	II/5	II/8	II/4	III/8	II/2	II/3	II/1
Root Weight	III/6	II/2	II/5	III/4	III/2	II/1	II/4	II/7	III/3	II/3	II/8	III/1	II/6	III/5	III/7	III/8
Stem Weight	III/6	III/2	III/4	III/5	II/6	III/3	III/7	II/5	II/7	III/1	II/8	II/4	II/2	II/1	III/8	II/3
Foliage Weight	III/6	III/2	II/6	III/7	II/7	II/5	III/3	II/2	III/5	III/4	II/4	II/1	II/8	III/1	III/8	II/3
Total Weight	III/6	III/2	III/4	II/5	II/2	III/3	II/6	III/5	II/7	II/4	II/1	III/1	III/7	II/8	II/3	III/8
Shoot:Root Ratio	III/7	III/8	III/6	III/5	III/2	II/6	III/3	III/1	III/4	II/7	II/8	II/5	II/3	II/4	II/2	II/1

Plots are ranked in descending order

Plots underscored by the same line are not significantly different at 5% Level

Table 14. Matrix of Pearson Correlation Coefficient for clonal nutrient contents (mg/plant) prior to planting and growth during the first growing season in the field. (n = 10 and 16 for nutrient levels and morphological traits, respectively).

Morphological Traits	N	P	K	Ca	Mg
			After One Growing Season		
Height	-0.138 **	-0.166 **	-0.236 ***	-0.075 n.s.	-0.125 *
Root Collar Diameter	-0.188 ***	-0.188 *	0.057 n.s.	-0.111 *	-0.005 n.s.
Root Weight	0.139 **	0.253 ***	0.448 ***	0.273 ***	0.242 ***
Stem Weight	-0.018 n.s.	0.052 n.s.	0.254 ***	0.080 n.s.	0.121 *
Foliage Weight	-0.149 **	-0.093 n.s.	0.057 n.s.	0.010 n.s.	0.156 **
Total Biomass	0.012 n.s.	0.108 *	0.322 ***	0.156 **	0.199 ***

Significance Levels: ***, 0.1%; **, 1.0%, *, 5.0%; n.s., not significant (d.f. = 90)

Table 15. Relative increments of height and root collar diameter and weight gains of the average plant from each clone (n = 16).

Clone	Family A	B	C	E	F	G	H	I	L	M
					Height Increments (%)					
1	35.4	37.7		40.3	36.4	41.1		39.7	27.8	38.7
2	29.0	40.0	30.0	35.3	34.6	27.0	37.3	40.0	46.7	27.8
3	33.5	31.3	34.8	36.9	42.4	67.1	34.4	33.4	29.6	35.0
4	24.6	51.0	35.7	40.3	38.0	63.8	64.1	57.5	33.0	33.4
5	24.4	30.7	53.8	40.8		45.9	63.4	37.3	24.8	41.7
6	34.1	34.1	24.6	23.8	80.5	34.1	34.7	53.3	42.1	40.9
7	25.7	36.6	50.1	35.6	59.9	34.9	41.7	36.2	49.9	40.7
8	33.7	-	27.5	31.4	40.8	45.6	34.0	39.0	29.3	51.3
9	24.7	-	32.4	42.4		24.9	51.4	44.0	27.1	46.7
10	37.5	27.6	40.4	34.7	43.1	34.0		74.0	34.2	27.8
Mean	30.2	36.1	36.6	36.2	44.7	41.8	45.4	45.3	34.5	38.4
					Root Collar Diameter Increments (%)					
1	119.9	94.3		121.1	111.8	114.7		84.9	117.7	102.2
2	130.6	82.4	136.0	104.3	83.8	115.8	93.6	86.3	93.3	112.5
3	112.3	110.8	121.5	95.3	80.1	107.4	67.5	90.8	113.7	126.2
4	108.6	106.6	91.7	122.6	80.2	83.6	102.6	101.5	96.8	93.5
5	111.4	114.7	90.5	142.7		79.1	79.6	78.0	99.2	102.6
6	95.6	84.9	112.0	110.0	105.5	84.2	88.6	99.1	115.3	103.9
7	96.5	108.8	103.3	128.5	93.2	123.3	90.6	80.2	119.6	110.7
8	106.8	-	104.9	101.8	116.9	101.7	70.3	107.6	116.7	95.4
9	116.8	-	120.4	109.8		112.0	87.2	80.2	121.4	101.0
10	114.4	85.3	95.3	104.8	104.5	88.2		71.6	122.3	117.0
Mean	110..2	98.5	108.4	114.1	96.4	101.0	85.0	88.0	111.6	106.5

Table 15. (Continued).

Clone	A	B	C
1	353.2	314.8	
2	328.3	306.9	440.9
3	352.2	273.1	368.0
4	280.5	277.9	345.6
5	360.0	302.0	278.1
6	271.5	189.7	235.6
7	315.2	328.1	319.4
8	359.0		378.0
9	361.7		410.4
10	315.2	334.3	471.4
Mean	329.7	290.8	360.8
1	331.3	335.9	
2	395.6	487.7	406.2
3	374.8	289.4	438.0
4	271.3	297.5	363.4
5	292.8	381.4	487.9
6	285.2	340.4	300.9
7	200.6	364.3	484.1
8	366.2		324.0
9	308.5		388.4
10	409.3	247.6	422.3
Mean	323.5	343.0	406.6

Family						
E	F	G	H	I	L	M
Root Weight Gain (%)						
395.1	387.1	210.4		341.6	286.2	306.2
388.4	289.1	237.6	212.3	300.3	258.6	212.6
304.0	371.7	291.8	187.2	246.3	262.7	301.9
323.6	291.6	272.6	252.1	298.7	233.8	319.3
395.2		168.4	280.8	199.2	274.8	294.0
364.0	210.0	319.6	268.3	348.5	352.8	330.3
401.7	260.0	371.8	287.0	257.8	327.7	321.6
285.6	259.5	256.2	178.2	287.6	322.7	309.3
277.5		284.0	206.5	248.9	393.1	334.1
371.0	392.3	251.8		174.6	367.4	328.1
350.6	314.2	266.4	234.0	270.3	307.9	305.7
Stem and Branches Weight Gain (%)						
518.6	412.7	389.5		344.3	315.1	332.7
366.3	221.7	263.7	338.9	386.7	400.1	377.7
316.6	363.7	365.8	265.2	314.4	348.1	332.3
434.8	304.8	452.7	502.9	417.4	303.2	352.5
616.2		332.7	421.1	280.8	286.9	363.1
295.5	717.9	401.5	294.7	487.4	520.6	338.8
452.0	477.7	524.6	398.6	373.2	528.2	403.7
306.0	353.5	481.2	317.6	454.0	359.8	520.9
410.5		321.9	387.8	327.6	331.1	357.7
349.4	427.6	396.2		358.1	460.3	304.9
406.6	389.5	393.0	365.8	374.4	385.3	368.4

Table 15. (Continued)

Clone	A	B	C
1	117.6	171.4	
2	156.0	319.3	178.8
3	200.5	115.0	213.0
4	109.0	382.4	184.9
5	97.5	198.1	219.5
6	117.1	117.3	110.2
7	69.0	180.5	242.6
8	155.4		156.9
9	116.4		119.0
10	190.4	114.9	308.7
Mean	132.9	199.8	201.5
1	262.6	271.1	
2	288.9	347.1	333.6
3	302.7	221.8	335.6
4	214.8	449.4	292.8
5	240.1	289.4	313.4
6	220.7	206.4	212.4
7	182.5	288.1	342.0
8	290.2		279.4
9	254.6		327.8
10	299.2	226.2	399.4
Mean	255.6	287.4	313.6

Family						
E	F	G	H	I	L	M
Foliage Weight Gain (%)						
248.4	235.5	99.7		216.0	70.2	144.2
231.7	141.1	104.0	83.8	238.5	187.9	152.0
163.0	221.3	303.2	104.0	143.4	125.6	168.1
218.5	167.7	186.6	177.5	242.3	98.4	159.1
262.1		106.3	192.4	142.4	108.1	138.2
135.9	323.5	198.7	130.0	261.8	263.2	189.3
266.7	243.5	212.8	137.3	180.1	189.2	224.1
118.8	152.3	205.7	75.8	221.0	183.2	254.6
154.5		98.9	111.6	150.6	155.4	149.2
196.1	202.6	147.2		218.4	206.1	135.4
199.6	203.4	166.3	126.5	201.5	158.7	171.4
Total Weight Gain (%)						
379.5	340.2	222.7		300.0	217.2	258.0
326.2	213.1	197.6	208.5	302.2	277.0	233.3
258.1	316.4	410.9	181.2	230.3	241.2	263.7
321.1	249.3	291.0	293.9	346.0	209.3	274.0
410.9		193.3	287.3	202.6	219.5	258.6
258.0	360.7	301.3	228.4	356.4	367.6	281.9
370.0	312.6	356.6	267.4	262.7	326.2	311.5
233.2	251.2	297.7	180.3	305.3	285.0	341.7
275.9		229.2	226.4	239.6	283.4	273.8
303.0	336.8	251.3		259.1	336.8	251.3
293.3	293.3	274.4	234.2	280.4	276.3	274.8

68 - 143%; root weights 168 - 471% and total plant weights 181 - 449%, respectively.

As in the case of absolute growth, Families C and E had the highest relative growth rates and Family H ranked lowest; an exception existed for relative height growth. For example Clone 4 of Family E exhibited some of the highest relative gains in root, stem, foliage and total plant weights, but its relative height growth was comparable to that of the least performing clone, e.g. Clone 8 of Family H.

Variation in relative growth was about as large within as among families.

NUTRIENT UPTAKE

Similar to the determination of elemental content prior to planting, nutrient and Al uptake was determined after one growing season by chemical analysis of plant components. According to the results (Tables 16 and 17), the uptake of all elements was strongly influenced by family, clones and plot.

Family Effects

The family factor comprised from about 9% to 29% of the total variance, depending on element (Table 18). As earlier indicated, there was no significant family effect on pre-planting nutrient contents, except for K (Table 6). It is interesting to note that the family factor

Table 16. Mean nutrient uptake (mg/plant) by families and clones (n = 4).

Clone	Family A	B	C	E	F	G	H	I	L	M
					Nitrogen					
1	112.92	97.26	25.36	121.20	135.32	79.84	-	132.60	101.81	135.70
2	144.56	91.70	155.55	140.02	102.43	122.62	108.45	137.00	128.13	55.68
3	123.16	118.14	173.59	153.47	129.44	107.00	65.28	107.24	99.51	115.51
4	128.52	75.14	123.26	184.11	91.41	76.22	114.13	86.65	118.43	121.48
5	170.26	113.97	118.46	140.77	-	75.68	113.13	102.45	102.52	102.06
6	96.18	65.29	129.52	161.91	94.62	123.41	110.93	141.20	131.40	89.22
7	112.77	121.29	148.12	173.94	108.45	146.07	121.64	108.21	85.53	121.82
8	117.69	-	148.42	121.20	120.11	115.53	75.75	94.13	121.63	94.72
9	151.33	-	179.01	129.53	-	156.58	92.64	96.92	149.25	115.29
10	115.84	122.99	156.51	129.54	129.25	86.14	-	78.04	135.94	137.66
Mean	127.32	100.72	144.74	145.49	115.16	108.91	100.29	108.44	117.42	108.91
					Phosphorus					
1	10.75	11.05	3.20	12.14	12.66	9.02	-	11.46	10.72	11.84
2	13.85	9.49	15.89	15.12	10.17	12.19	11.60	12.18	11.68	5.30
3	10.99	11.75	16.56	15.43	13.53	10.27	6.15	10.01	11.00	10.99
4	13.53	7.93	12.73	19.83	8.86	7.39	10.57	8.02	12.04	12.18
5	15.29	11.22	11.55	15.53	-	7.92	10.72	9.71	9.16	9.68
6	10.27	6.28	12.11	15.99	9.75	12.10	10.68	15.14	13.74	7.31
7	10.18	10.83	14.85	16.55	10.31	15.61	10.09	10.15	8.76	12.60
8	11.17	-	15.37	11.81	12.79	11.13	6.43	8.38	12.81	9.48
9	13.89	-	16.98	12.52	-	15.00	8.34	9.88	14.37	10.80
10	9.79	12.48	14.88	13.99	14.97	7.64	-	7.49	15.49	12.19
Mean	11.97	10.13	14.24	14.89	11.76	10.83	9.32	10.24	11.98	10.24

Table 16. (Continued).

Clone	Family A	B	C	E	F	G	H	I	L	M
					Potassium					
1	28.31	18.43	6.11	29.50	24.66	15.88	-	21.33	24.01	26.91
2	35.00	19.04	37.21	31.60	16.57	21.64	15.91	21.60	24.53	8.81
3	23.05	21.43	35.93	31.54	27.92	23.15	14.21	12.20	27.64	19.91
4	28.18	17.67	29.51	64.79	14.48	23.47	21.32	18.67	26.65	22.77
5	21.61	22.93	23.62	42.47	-	18.33	20.42	17.58	22.13	18.62
6	21.33	9.29	19.65	27.22	18.20	25.21	12.38	25.03	33.04	26.19
7	17.01	26.08	27.05	44.12	22.32	36.34	22.29	17.88	19.72	23.05
8	27.13	-	36.81	29.64	20.04	23.32	14.35	17.85	25.80	21.82
9	29.90	-	37.97	27.07	-	24.17	14.38	20.56	25.64	20.45
10	23.62	17.26	30.99	35.97	28.37	13.13	-	14.59	29.00	24.98
Mean	25.52	19.01	30.29	36.35	21.80	22.46	16.91	18.73	25.82	21.35
					Calcium					
1	33.40	29.27	5.50	37.35	35.86	19.58	-	30.98	33.32	33.36
2	32.96	27.65	41.91	38.00	24.35	27.98	27.79	26.17	25.40	27.30
3	29.27	33.43	35.07	35.36	37.08	29.47	23.33	23.22	27.77	27.33
4	30.31	29.27	28.55	55.90	30.41	27.94	33.89	20.57	32.52	36.76
5	40.48	29.86	31.00	39.39	-	21.22	33.36	29.18	25.54	32.43
6	29.34	32.29	31.94	45.98	20.62	33.08	30.37	40.71	31.37	21.28
7	35.72	30.80	32.41	39.99	26.60	34.63	37.61	26.84	26.99	31.04
8	34.11	-	34.23	35.46	29.58	29.67	29.37	24.14	31.28	37.26
9	41.06	-	37.21	28.81	-	46.68	34.04	18.82	33.50	30.33
10	29.58	36.89	27.44	37.67	32.06	24.93	-	22.11	37.59	33.32
Mean	33.39	31.56	32.57	39.39	30.17	29.52	31.22	26.27	30.53	31.06

Table 16. (Continued).

Clone	Family A	B	C	E	F	G	H	I	L	M
					Magnesium					
1	27.12	9.32	2.00	9.27	15.89	7.17	-	29.12	12.87	13.83
2	26.87	15.56	23.55	21.67	9.80	10.09	6.97	14.59	7.65	5.09
3	15.14	12.59	22.48	16.26	12.91	10.43	10.09	12.73	12.95	5.89
4	14.96	12.31	21.42	28.50	9.91	17.80	13.13	9.04	11.74	11.24
5	21.88	7.39	14.47	19.85	-	4.97	16.51	14.53	7.89	12.86
6	14.73	6.53	13.21	26.87	6.66	24.90	9.91	25.86	12.59	9.12
7	20.22	9.79	20.89	29.97	11.25	11.41	17.28	7.12	12.93	10.33
8	38.67	-	21.31	11.93	8.92	17.97	7.86	6.98	9.75	6.45
9	31.49	-	19.05	15.69	-	21.49	14.51	5.42	15.09	8.03
10	17.38	17.46	11.86	19.19	10.51	4.72	-	8.49	13.92	18.82
Mean	22.84	11.34	18.22	19.92	11.00	13.09	12.01	13.40	11.74	10.17
					Aluminum					
1	11.32	3.08	0.06	3.58	5.44	2.51	-	10.41	3.42	5.42
2	8.12	6.22	8.49	7.76	3.99	3.96	2.66	5.91	2.42	1.54
3	5.41	4.23	7.63	7.54	5.87	3.40	5.69	3.94	4.79	1.62
4	5.44	4.46	6.68	10.04	4.11	5.79	3.81	3.44	4.26	4.49
5	7.91	4.97	4.69	5.28	-	2.15	5.52	4.52	2.11	5.31
6	8.73	2.00	4.45	9.16	0.64	8.88	3.59	7.72	4.91	3.43
7	7.85	3.74	5.69	9.55	3.67	4.13	7.13	2.09	4.34	3.59
8	11.86	-	7.42	6.41	2.59	4.93	2.88	2.16	3.20	2.58
9	10.99	-	7.28	5.12	-	6.98	5.05	2.78	5.63	2.39
10	5.04	6.05	4.38	5.89	4.57	3.39	-	2.86	4.12	6.63
Mean	8.27	4.34	6.13	7.03	4.08	4.61	4.54	4.58	3.92	3.70

Table 17. Result of the analysis of variance for nutrient uptake per plant.

Source of Variation	Degrees of Freedom	N	P	K	Ca	Mg	Al
		F-Ratio					
Plot	3	41.93***	25.57***	35.77***	103.14***	15.19***	12.13***
Family	9	3.99***	4.88***	7.98***	3.68***	5.25***	5.75***
Clone (Family)	84	4.35***	5.08***	4.39***	3.80***	3.82***	2.97***
E.M.S.	274						

Significance Levels: ***, 0.1%; **, 1.0%; *, 5%; n.s., not significant

Table 18. Absolute variance components (V.C.) and percent of total variance (%) for uptake of N, P, K, Ca, Mg and Al. (Computations based on expected mean square.)

Variance Component	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Aluminum	
	V.C.	V.C.%	V.C.	V.C.%	V.C.	V.C.%	V.C.	V.C.%	V.C.	V.C.%	V.C.	V.C.%
Plot	220.26	16.54	1.15	9.13	13.43	12.24	36.15	36.13	5.32	6.65	0.58	5.69
Family	216.24	16.24	2.75	21.83	31.31	28.54	8.78	8.77	15.96	19.94	1.99	19.55
Clone (Family)	410.87	30.86	4.42	35.08	30.04	27.38	22.89	22.88	24.52	30.63	2.54	24.95
Error	483.92	36.36	4.28	33.96	34.91	31.84	32.22	32.22	34.24	42.78	5.07	49.81
Total	1331.29	100.00	12.60	100.00	109.69	100.00	100.04	100.00	80.04	100.00	10.18	100.00

attained its largest variance component for K uptake (Table 18). Ranking of families with respect to nutrient uptake (Table 19) resulted in similar patterns as ranking according to growth, i.e plants of the fastest growing families showed highest nutrient uptake.

Nitrogen uptake for plants of Family E increased the pre-planting N content, by a factor of about 7. The initial P content of the plants was increased in the same plants by a factor of 4.1 (Tables 5 and 16). Similarly, the average plant of Family E increased its K and Ca contents by factors of 2 and 3, respectively. Contrasting with uptake responses in Family E, the average plant in Family H increased its N, P, Ca and Mg contents only by a factors of 4, 2.5, 1.1 and 2.4, respectively. (Tables 5 and 16).

Clonal Effects

The mean clonal N uptake ranged from 55.68 mg to 184.11 mg per plant and that of P from 5.30 mg to 19.83 mg per plant. Some clones had eight times more K than others. Similarly, wide ranges were found for Ca (18.8 - 55.9 mg per plant) and Mg (11.9 - 38.7 mg per plant). Uptake of Al varied from 1.54 to 10.04 mg per plant (Table 16).

As in the case of growth, clones contributed more to the variance of nutrient uptake than families, except for K (Table 18). Clone 4 of Family E, which was previously singled out as the best performing genotype, also had the highest uptake of N, P, K, and Ca (Table 16). Clones 6 and 7 of Family E also ranked high on the scale of

Table 19. Ranking of families (A-M) according to total nutrient and Al uptake (mg/plant) after one growing season (Duncans Multiple Range Test).

Nutrient	Rank									
	1	2	3	4	5	6	7	8	9	10
Nitrogen	E	C	A	L	F	M	G	I	B	H
Phosphorus	E	C	L	A	F	G	I	M	B	H
Potassium	E	C	L	A	G	F	M	B	I	H
Calcium	E	A	C	B	H	M	L	F	G	I
Magnesium	A	E	C	I	G	H	L	B	F	M
Aluminum	A	E	C	G	I	H	B	F	L	M

Families ranked in descending order
Families underscored by the same line are not significantly different at 5% Level

nutrient uptake. In contrast, Clone 8 of Family H, which had shown poor growth, was among the worst six clones with respect to N, P and K uptake. The rate of Al accumulation tended to be highest in the fast-growing plants.

Plot Effects

It should be recalled that plants representing any one clone on four adjacent plots were pooled into one sample. Accordingly, plot in the present context, refers to the area given by four adjacent original plots. For example, the enlarged plot 3 is composed of the original adjacent plots III/1, III/2, III/5 and III/6 (Figure 4).

As shown by the analysis of variance, the composite plots were a significant source of variation (Table 17), but their variance components were, more often than not, smaller than those listed for families and clones (Table 18). Nitrogen and P uptake were highest and Ca, Mg, and Al uptake were lowest on the enlarged plot 3. As shown earlier, the original plot III/6 supported the best plant growth.

CORRELATION BETWEEN GROWTH VARIABLES AND NUTRIENT UPTAKE

According to Table 20, root collar diameter and component plant weights were significantly correlated with the uptake of all elements. The closest correlations were observed for total plant

Table 20. Matrix of Pearson correlation coefficient between morphological traits and nutrient uptake at clonal level (n=4 and 16 for nutrient levels and growth variables, respectively).

Variables	N	P	K	Ca	Mg	Al
Height	0.054 n.s.	0.066 n.s.	0.088 n.s.	-0.081 n.s.	-0.048 n.s.	-0.024 n.s.
Root Collar Diameter	0.637 ***	0.649 ***	0.384 ***	0.395 ***	0.172 ***	0.179 ***
Root Weight	0.779 ***	0.764 ***	0.681 ***	0.602 ***	0.622 ***	0.592 ***
Stem Weight	0.824 ***	0.805 ***	0.602 ***	0.298 ***	0.313 ***	0.267 ***
Foliage Weight	0.776 ***	0.763 ***	0.679 ***	0.251 ***	0.327 ***	0.282 ***
Total Weight	0.911 ***	0.892 ***	0.743 ***	0.458 ***	0.494 ***	0.449 ***
N		0.911 ***	0.648 ***	0.448 ***	0.403 ***	0.381 ***
P			0.681 ***	0.431 ***	0.414 ***	0.381 ***
K				0.611 ***	0.529 ***	0.428 ***
Ca					0.588 ***	0.417 ***
Mg						0.843 ***
Al						

Significance Levels: ***, 0.1%; **, 1.0%; *, 5.0%; n.s., not significant (d.f.=90)

weight and N uptake (r = 0.911) and total plant weight and P uptake (r = 0.892). Height growth showed no correlation with element uptake.

Nitrogen and P uptake were very closely correlated with each other (Table 20). A close correlation was also observed between Al and Mg uptake.

ALUMINUM ACCUMULATION

While more than half of the nutrient amounts absorbed by the roots were translocated to the shoots, 90% to 97% of the absorbed Al was retained by the roots (Table 21).

According to Table 19, there were significant differences among families for Al uptake . Plants of Families A, E, and C showed the highest and plants of Family M the lowest Al uptake. Uptake of Al was significantly correlated with plant weight, but it should be noted that the correlation was closer with root biomass (r = 0.592) than total plant weight (r = 0.449) (Table 20). Slow growing families, as for example H, I, and B had relatively less Al accumulation in their roots and foliage than the fast growing families (Table 21).

NUTRIENT USE EFFICIENCY

Nutrient use efficiency is generally defined as the quantity of dry matter produced per unit weight of nutrient element taken up

Table 21. Aluminum content (mg/plant) of roots, stems and foliage by family after one growing season.

Families	Foliage	Stem	Roots
A	0.188	0.121	7.96
B	0.174	0.097	4.07
C	0.206	0.146	5.95
E	0.254	0.199	6.58
F	0.152	0.105	3.82
G	0.181	0.123	4.31
H	0.122	0.115	4.31
I	0.157	0.098	4.33
L	0.211	0.128	3.58
M	0.158	0.114	3.43

(Van den Driesche 1974). In the present study, nutrient use efficiency was determined by dividing the gain in plant weight by the net gain of a given element. Plants of family E, which were earlier identified as fast growers, had high N use efficiency and intermediate P, Ca and Mg use efficiencies but these plants were among the least efficient K utilizers (Table 22). Similar trends were observed for Families A and L.

In contrast, the families that were earlier considered slow growers (B, I and H), had below average N use efficiency, intermediate P and Mg use efficiency and high K use efficiency. The ranges for nutrient use efficiencies were considerably wider for clones than families. Use efficiencies for N and P ranged from 46 to 87 and from 421 to 897, respectively. Potassium and Ca, on the other hand, ranged from 166 to 483 and from 103 to 327, respectively. The range was widest for Mg use efficiency 205 to 1222 (Table 22).

Clone 4 of Family E, which was ranked highest for growth and nutrient uptake, was considered intermediate in N, P, Ca and Mg use efficiency. Clone 8 of family H, a poor performer, had below average N and K use efficiencies and was further characterized by high Ca concentrations in its tissues (Table 22).

Table 22. Nutrient use efficiency given by family and clone after one growing season.

CLONE	FAMILY A	B	C	E	F	G	H	I	L	M
					Nitrogen					
1	66.16	61.63	47.25	65.02	56.39	60.71	71.94	52.41	71.32	59.10
2	66.37	54.31	64.76	65.07	55.37	58.25	59.13	49.78	56.44	69.78
3	65.80	64.10	56.08	58.08	59.66	58.50	73.47	60.17	70.65	62.34
4	62.10	63.38	55.52	58.34	59.74	75.72	53.99	65.13	60.73	57.50
5	53.35	60.32	54.56	63.75	67.85	58.47	56.50	51.56	63.22	62.45
6	62.64	54.22	54.83	65.10	62.47	62.16	53.92	55.88	60.73	73.54
7	57.32	61.63	56.25	59.86	55.54	60.00	54.77	55.08	64.33	58.54
8	67.09		60.04	57.59	55.37	52.99	55.35	59.72	62.50	63.36
9	64.90		57.21	56.83	87.28	50.22	54.97	63.57	55.97	55.47
10	59.24	58.01	50.42	68.26	48.76	57.14	46.29	61.28	61.22	58.07
Mean	62.50	59.70	55.69	63.72	60.84	59.42	58.03	57.46	62.71	62.01
					Phosphorus					
1	694.88	542.08	448.48	649.09	602.69	534.37	608.18	579.17	677.24	677.36
2	692.42	524.76	633.73	602.51	557.52	584.91	552.11	559.93	619.01	732.08
3	737.03	644.26	587.56	577.45	570.60	609.54	778.86	644.36	639.09	655.14
4	589.80	600.25	537.31	541.60	546.00	780.78	582.78	703.24	597.18	573.07
5	593.85	612.30	559.31	577.59	631.00	558.08	596.08	543.77	707.42	658.06
6	586.17	562.10	586.29	659.16	606.15	633.88	559.93	521.14	580.79	897.40
7	634.58	689.75	560.94	629.00	583.90	561.18	660.06	587.19	627.85	565.87
8	706.36		579.70	591.02	519.94	549.87	651.63	670.64	593.29	632.91
9	706.98		603.06	587.86	749.17	524.00	610.31	623.48	581.07	591.67
10	700.72	571.31	530.24	631.88	420.84	643.98	470.00	638.18	537.12	624.71
Mean	664.28	593.35	562.66	604.72	578.78	598.06	606.99	607.11	616.01	660.83

Table 22. (Cont.)

CLONE	A	B	C	E	FAMILY F	G	H	I	L	M
					Potassium					
1	263.86	325.01	968.90	267.12	309.41	303.53	318.57	325.83	302.37	298.03
2	274.00	261.55	270.63	288.29	342.18	329.48	402.89	315.74	294.74	440.41
3	351.41	353.24	270.80	282.50	276.50	270.41	337.09	528.69	254.34	361.63
4	283.18	269.38	231.79	165.77	377.07	245.85	288.93	302.09	269.79	281.79
5	420.18	299.61	273.50	211.21	371.18	241.13	312.93	300.34	292.82	342.11
6	282.23	379.98	361.32	387.22	324.73	217.84	483.04	315.22	241.53	250.48
7	379.78	275.85	307.95	235.95	269.71	241.06	298.79	333.33	278.90	309.33
8	290.82		242.05	235.49	331.84	262.44	291.99	314.85	294.57	274.98
9	328.43		269.69	253.18	390.87	325.20	353.96	299.61	325.66	312.47
10	290.43	413.09	254.60	245.76	222.07	374.71	321.58	327.62	286.90	319.86
Mean	316.43	322.22	345.12	257.25	321.56	281.16	340.98	336.33	284.16	319.11
					Calcium					
1	223.65	199.87	232.16	210.98	212.77	246.67	290.87	224.34	217.89	240.41
2	290.96	180.11	240.28	239.74	232.85	254.82	230.66	260.60	284.65	142.12
3	276.73	226.44	277.45	251.98	208.20	212.42	205.32	277.78	253.15	263.45
4	263.28	162.62	239.58	192.13	179.55	206.51	181.76	274.19	221.09	189.88
5	224.31	230.07	208.39	227.72	233.70	208.29	191.55	180.95	253.72	196.42
6	205.18	102.95	222.29	229.23	286.61	231.86	196.90	193.81	254.38	308.27
7	180.85	242.53	257.02	260.32	226.32	252.96	177.08	222.06	203.78	229.70
8	231.31		260.30	196.84	224.81	206.27	142.66	232.81	242.97	161.03
9	239.16		275.19	255.47	299.67	168.38	149.53	327.31	249.25	210.68
10	231.91	193.28	287.54	235.04	196.51	197.35	290.95	216.19	221.34	239.80
Mean	236.74	192.23	250.02	229.94	230.10	218.55	205.73	241.00	240.22	218.18

TABLE 22. Continued

CLONE	FAMILY A	B	C	E	F	G	H	I	L	M
					Magnesium					
1	275.44	642.70	493.33	850.05	480.18	672.25	557.50	238.67	564.10	579.90
2	356.90	320.05	427.60	420.40	578.57	706.64	919.66	468.09	945.10	762.28
3	535.01	601.27	432.83	547.97	597.99	600.19	474.73	506.68	542.86	1222.41
4	533.42	386.68	319.33	376.84	550.96	324.16	469.15	623.89	612.44	621.00
5	414.99	929.63	446.44	451.89	631.00	889.34	387.04	363.39	821.29	495.33
6	408.69	540.58	537.47	392.26	887.39	308.03	603.43	305.10	633.84	719.30
7	319.49	763.02	398.76	347.30	535.11	767.75	385.42	837.08	425.37	690.22
8	204.03		418.11	585.08	745.52	340.57	575.55	805.16	779.49	930.23
9	311.85		537.53	469.09	899.00	365.75	350.79	1136.53	553.35	795.77
10	394.71	408.36	665.26	460.66	599.43	1042.37	470.00	563.02	597.70	424.55
Mean	375.45	574.04	467.67	490.15	650.51	601.70	519.33	584.76	647.55	724.10

DISCUSSION

The results of this study have confirmed the hypothesis that black spruce varies significantly within and among half-sib families with respect to nutrient uptake and use efficiency after field planting. Considering nutrient uptake, families varied by a factor of 1.45 to 2.25 depending on element, and clones within families by a factor of 2.40 to 8.19, depending on family and nutrient element. In comparison, variation in growth variables was usually smaller. This may indeed reflect genetic differences in nutrient uptake ability and use efficiency as predicted from earlier greenhouse studies (Mullin 1984; Mallondo 1986; Cruickshank 1990).

PRE - PLANTING DIFFERENCES

Variation among and within families became apparent early in the rearing stage of the experimental stock. For example, clones from Families B and I were difficult to reproduce vegetatively from cuttings, and appeared to be more sensitive to low temperature during overwintering than clones from other families.

Similar observations have been reported elsewhere in the literature. Rauter (1971; 1974) noted not only varying rooting ability, but also differences in growth and form among Ontario black spruce clones. Also of interest in this connection are the results reported by

Phillion et al. (1982b) from the Ontario super-seedling program. In this case, two- to four-year- old black spruce seedlings were selected from the nursery bed for vegetative reproduction. Although the selected seedlings retained their superiority after planting, cuttings taken from them rooted poorly and survival was low.

With the variation in rooting ability of cuttings from plants of different genotypes, it is difficult to propagate stock that is uniform in size at the outset of an experiment. It would also be difficult to predict whether the initial differences will be retained, whether they will narrow or become wider after field planting.

In the present study, some of the clones with smaller plants responded more vigorously to the field enviroment than clones with originally larger plants, and moved thereby up in rank (Figure 7). The frequent changes in rank of clones during field growth may help to explain the low correlation coefficients for measurements of growth variables before and after the growing season (Table 12).

NUTRIENT UPTAKE EFFECIENCY

If shortage of an essential element has become a growth limiting factor, an important consideration is the efficiency with which the plants can extract this element from the soil.

Noggle et al (1960) defined root absorption capacity as the amount of a given element taken up per unit time and volume of root biomass. They observed significant differences in absorption capacity among both species and genotypes.

For the purpose of this study, nutrient uptake efficiency is determined as the amount of a given element absorbed by the plant during the first growing season. Shortage of N is assumed to be the primary limiting factor and shortage of P a secondary limiting factor. This assumption is based on the close correlation between biomass gain and N or P uptake (Table 20).

Differences in nutrient uptake efficiency have been attributed to variation in root development and activity (Saric 1983). In the present study, clones of Family E exhibited superior growth and the highest N uptake (Table 16). The average clonal root biomass increased during the field growth by about 350%. In comparison, clones of Family H, which grew least and accumulated the lowest quantities of N, increased their root biomass by only 230% (Table 15).

The importance of root growth response as a factor determining nutrient uptake efficiency has been supported by the findings from other studies. Goddard et al. (1976) demonstrated differential growth responses among families of slash pine to fertilization in a field trial. The best responses were shown by plants of those families which had produced the largest root biomass in a previous pot culture experiment. Mullin (1984) and Mallondo (1986) made similar observation with black spruce families. They noted that plants that responded best in overall growth to addition of nutrients were those which produced the largest root biomass.

Varieties and species with low relative height growth tend to have a proportionately large root biomass because of a shift in the allocation of photosynthate (Chapin 1980). This also is of interest in

connection with the present study as clones of Family H showed both the best relative height growth and the least relative root growth. For clones of Family E, this relationship was reversed.

The emphasis on nutrient uptake efficiency as a criterion to distinguish genotypes is further supported by the work of Miller (1984) who reported significant correlations between net productivity of conifer genotypes and accumulation of N and P in the above ground biomass. He suggested that the difference in biomass gain among genotypes was largely due to differences in nutrient uptake efficiency.

The results from the present experiment generally agree with previously published information , and it would be reasonable to conclude that clones with the highest relative root growth, had the highest nutrient uptake efficiency.

NUTRIENT USE EFFICIENCY

Nutrient efficient genotypes are those which produce the largest amounts of biomass per unit of element taken up (Clark 1983). According to Graham (1984), a nutrient efficient genotype is one which has the ability to produce a high yield in a soil with a limited nutrient supply.

In the present study, fast growing families, as for example E, A and L, excelled in both high N and P uptake ability and high N use efficiency. The slow growing families H, I and B had low N and P use efficiency, but a high K use efficiency (Table 22).

According to Rorison (1968), Grundon (1972) and Harison et al. (1979), slow growing genotypes retain high tissue nutrient concentrations even under conditions of low nutrient supply. In contrast, rapidly growing genotypes show low tissue concentration, i.e. they display high use efficiency which is often associated with the appearance of visual symptoms of deficiency (Nassery 1970; Brix 1971; Grundon 1972). Defined in this way, high nutrient use efficiency is one of the mechanisms by which plants adapt to sites of low fertility (Grundon 1972; White 1973).

Another criterion for nutrient use efficiency is the rate of translocation of nutrients within the plant, i.e., from senescent and less active tissue to growing regions. Fife and Nambiar (1984) reported that the internal translocation in young radiata pine accounted for 66, 48 and 39 percent of the annual P, N and K requirements. It should be pointed out that these observations were made with older trees which replace a large proportion of their needles each year. The amount of needles shed by rapidly growing young trees is small compared to the amounts of new needles formed in the same year. Thus internal cycling may not have been a significant factor in genotypes identified as nutrient efficient in this study.

Based on his experience with agricultural crops, Graham (1984) pointed out that no single genotype has yet been found to be efficient with respect to more than one nutrient element, because in each case efficient use is based on specific major-gene inheritance.

Woessner et al.(1975) working with conifers further pointed out that the capacity of a genotype to accumulate one element does not necessarily confer to it the capacity to accumulate another.

ALUMINUM ACCUMULATION

As observed in earlier work (Mallondo 1986, Cruickshank 1990, Truman et al. 1986), the plants in the present study had accumulated appreciable amounts of Al in the roots, but concentrations in the foliage were low. Plants of Families A, E, and C, which showed the highest rates of growth, had the largest Al accumulation in the roots, but not always the highest foliar Al concentrations (Table 21). Preventing translocation of Al from roots to shoots has been suggested as one of several mechanisms leading to the development of Al tolerance in plants (Foy and Fleming 1978; Foy 1988; Taylor 1988).

According to work with agricultural species the absorbed Al accumulates in the root free-space (Rorison 1965; Wright 1989). It appears that plants of all families and clones from the present study were able to prevent excessive translocation of Al to the shoots (Table 21).

High Al content of the roots could also be seen to reflect high P uptake. It is important to recall that uptake of P and Al were indeed positively correlated with each other. This should not be unexpected as P is likely to exist and move as a complex Al-phosphate ion in the soil solution of strongly acid soils (Larson 1967). Furthermore, uptake of such ions by roots has been demonstrated in the literature (Larson

1967). With this understanding, the most effective plant on acid soils is one that effectively assimilates Al-phosphates and immobilizes the Al in the roots while phospate is being translocated into the shoots. This agrees with Salinas and Sanchez (1976) statement that the ability of plants to absorb and translocate P at high levels of Al in the roots determines their tolerance to low P availability. This is further supported by the recent work of Cruickshank (1990).

CONCLUSIONS

The following conclusions are drawn from the results of this study:

1. Early field growth of vegetatively reproduced black spruce varied strongly among half-sib families and clones within half-sib families.
2. The fast growing plants exhibited superior root development. This was reflected by larger than average root biomass per plant and lower than average shoot:root ratios.
3. Biomass accretion was closely correlated with N and P uptake. Based on these relationships, and on needle responses to fertilization in the following year (not reported in this thesis), it was assumed that low N and P supply, especially low N supply, limited to varying degrees the growth of the plants.
4. The variation in growth among families and clones is attributed to the differences in N and P uptake efficiency which in turn depends on root development.
5. Phosphorus uptake was positively correlated with Al uptake. This further suggests that P was moved towards the roots as a complex Al-phosphate ion and that the efficiency of

plants to use P in this form is dependent on their ability to immobilize the Al in the roots, while translocating the phosphate to growing points above and below ground.

6. Most genotypes that were classified as fast growers, e.g. Clones 4, 6, and 7 of Family E, also had high N and/or P use efficiency, which is expressed as the amount of biomass produced per unit of nutrient element taken up.
7. Genetic differences in rate of growth and nutrient uptake are evident early in the rearing stage of the planting stock. This makes it difficult to obtain uniform plants by vegetative reproduction for field experiments.
8. The present investigation is part of an experiment which is in its initial stages. Continued monitoring of growth and mineral nutrition is required to verify the above conclusions.

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APPENDIX

APPENDIX I

Expected low, critical and adequate concentrations of elements in foliage of conifers (From Morrison, 1974).

Species	Concentration (% Oven dry weight)		
	Low	Critical	Adequate
		Nitrogen	
Picea mariana	1.20	1.20-1.50	1.50+
		Phosphorus	
Picea mariana	0.14	0.14-1.50	0.18
		Potassium	
Picea mariana	<0.19	0.19-0.30	0.40-0.80
		Calcium	
Picea mariana	0.10	0.10-0.15	0.15
		Magnesium	
Picea mariana	0.09	0.09-0.12	0.12
		Manganese	
Picea abies	4.0-15.0	20.0	20.0

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