bili with celluloid tubes increased the proportion of empty seed in the final crop.

Premature abscission of conelets and cones caused serious loss of seed. A large proportion of conelets were shed in the weeks following pollination with losses continuing at a low rate until just before harvest in December of the following year when the rate of cone loss often increased. Between seventeen and eighty-five per cent of strobili pollinated abscissed before reaching maturity. Following wind pollination there was usually a greater loss of conelets and cones than after controlled pollination using stored pollen. After both wind and controlled pollination the rate trees was twice that on the south side.

A high rate of cone and conelet loss was associated with a high ratio of cone volume to number of seed per cone in the final crop. In this respect the clones studied appeared to form two sub-populations. In one, containing the longest number of clones, approximately forty-four per cent of the variation in total seed per cone and per cent full seed per cone was associated with cone loss. In contrast, in the other population where there was a smaller increase in cone and conelet loss as the ratio of cone volume to number of seed per cone increased, fifty per cent of the variation in "percent full seed per cone" was associated with cone volume.

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Growth and Nutrient Uptake of Aspen Hybrids Using Sand Culture Techniques

By **Dean W. Einspahr**[1])

Introduction

Projected forest industry raw material requirements and predicted forest land use trends have created considerable interest in intensive forestry practices. These projections emphasize the need for the production of species that will do well on low-quality sites and respond to improvements in soil fertility and soil moisture conditions. The study described is part of a larger comprehensive study under way aimed at evaluating the nutrient requirements of several types of aspen hybrids. The basic approach involves the use of sand culture techniques to compare the growth and nutrient requirements of aspen hybrids with comparable seedlings of the "parent species".

Recent tree nutrition studies, primarily with cottonwood (P. deltoides) and hybrids in the black poplar group (section Aigeiros) emphasizes that large growth increases result when optimum nutrient levels are maintained. Little data are available on the nutrient requirements of aspen and aspen hybrids. Nutrient deficiency symptoms described by **Hacskaylo** and **Vimmerstedt** (1967) have demonstrated the essential nature of a number of nutrient elements to the growth of cottonwood. **Bonner** and **Broadfoot** (1967) found cottonwood seedlings grew best when nutrient solutions contained 100 ppm N, 75 ppm P, and 100 ppm K. Similar optimum levels of N and K and a lower level of P (18—25 ppm) were reported by **Phares** (1966) for cottonwood grown using sand culture techniques under greenhouse conditions. Curlin (1967), in a study on 22 cottonwood clones, reported large increases in growth as a result of nitrogen fertilization and a strong "clone X fertilizer" interaction.

Satoo (1960) in N, K, and P sand culture studies with P. davidiana demonstrated the absence of nitrogen had the most serious influence on growth. Also of interest is the work of **Shumakov** (1963) who pointed out that aspen assimilates three to four times as much N, five times as much Ca, and four times as much P as pine. Cultivated poplars are reported to enrich the soil with humus and assimilated bases, such as Ca arid Mg, but deplete the soil of N. Other Russian work by **Slukhai** (1962) with poplar

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indicates that N, P, and K fertilization reduces the transpiration coefficient and results in more economical utilization of soil moisture.

Methods and Materials

A sand culture technique similar to that described by Swan (1963) was used to investigate the nutrient requirements of two aspen hybrids. To make it possible to compare the results from a series of experimental runs, the experimental work was carried out in a growth chamber. Basically, the system employed growth containers containing silica sand which were attached to pressurized carboys containing nutrient solutions. Every four hours a time clock activated a valve on the compressed air line which in turn caused the solutions to be pumped into the growth containers. After five minutes the valve closed and the solutions drained back into the carboys. Test seedlings were grown in the sand on this periodically fluctuated nutrient solution. One basic unit consisted of a pressurized carboy and three growth containers. Each growth container was a replication and each treatment was replicated a total of six times.

The overall plan for the entire study consisted of running a series of three interrelated growth experiments. Light, temperature, day length, and relative humidity were held constant in each of the three "growth chamber trials" while the level of a different soil nutrient was varied. Seed from four experimental sources was used as plant material for the study. *Table 1* lists the type of parentage involved for the four progeny groups used.

Olson's (1944) combination of required elements were modified to provide nutrient solutions to meet the requirements of this investigation. *Table 2* presents the composition of the standard solutions and the six levels of each element used, when that element was being varied in the growth chamber trial. Deionized water was added periodically to reservoir carboys to prevent concentration of the nutrient solutions. The solutions were replaced 18 and 32 days after the start of the experiment.

Each of the growth containers contained four seedlings, one seedling of each of the four types of test materials. Seeds were sown directly on the growth containers and thinned to a single seedling per location when they were six to eight days old. Growth on the complete nutrient solution was rapid and at forty days it was not unusual to have seedlings that were 15 to 20 inches tall. After forty days of growth, all surviving seedlings were washed from the growth containers and the green weight (fresh weight) obtained for the tops and the roots along with the ovendry weight of the tops. The ovendry tops from the genetically similar seedlings grown on the same nutrient solution were combined, ground in a Wiley mill and used in determining the levels of N, P, K, Ca and Mg. Standard procedures for plant tissue were used and the results expressed as percent of tissue dry weight[2]).

Table 1. — Parentage of test trees.

Expt. material number	Parentage (female × male)
1	bigtooth aspen × bigtooth aspen
2	bigtooth aspen × E. gray poplar
3	E. gray poplar × bigtooth aspen
4	E. gray poplar × E. gray poplar

Table 2. — Composition of nutrient solution, ppm.

Nutrient	Standard solution[1])	Six levels used in growth chamber trials					
		1	2	3	4	5	6
N	158	29	50	75	105	131	158
P	65	2	11	22	43	54	65
K	93	3	15	31	62	77	93
Ca	46	—	—	—	—	—	—
Mg	21	—	—	—	—	—	—

[1]) Olson's (1944) nutrient solution modified to meet the requirements of the study. Appropriate levels of micronutrients were included in the standard solutions.

The dry weight — green weight ratio of the tops was calculated for all the experimental data. There were no significant differences between types of test materials or between treatments in the dry weight — green weight ratio. In view of the relatively constant ratios, the total green weight of the plant was selected as the growth figure to be used in comparing treatment effects. A randomized block design was used in arranging the treatments within the growth chamber. Analysis of variance procedures were used to investigate treatment and test material differences in growth and nutrient uptake. Duncan's multiple range test (1955) was used to examine between-material and between-treatment differences when analysis of variance procedures revealed significant differences existed.

Results

Nitrogen Trial

Six levels of nitrogen (29, 50, 75, 105, 131, and 158 ppm) were employed and, as previously discussed, there were six replications of each treatment level. *Figure 1* illustrates the green weight changes that resulted when the level of nitrogen was varied. *Table 3* summarizes the total green weigth analysis of variance "F" test information for the nitrogen, phosphorus, and potassium trials. Comparing the growth data for the four types of materials, nitrogen levels above 105 ppm resulted in decreased growth of the seedlings. When treatment means were compared, Treatment 4 (105 ppm) quite consistently resulted in the best growth and Treatment 1 in the poorest growth. In most instances growth differences between Treatments 1, 2, and 3 and between Treatments 5 and 6 were not statistically significant. Materials 1, 3, and 4 responded in a very similar manner to increasing levels of nitrogen. Material 2 appeared to have the lowest nitrogen requirement, demonstrated the greatest decrease in growth due to higher than optimum nitrogen levels, and was the apparent cause for the highly significant "treatment × material" interaction shown for nitrogen in *Table 3*.

The nitrogen treatments used not only influenced growth but also influenced the uptake of N, P, K, Ca, and Mg. *Figures 2, 3, and 4* illustrate the influence the nitrogen treatments had on the levels of the other major essential elements in the tops of the experimental seedlings. These data indicate there was increased nitrogen uptake as the level of nitrogen in the nutrient solution increased up to 105 ppm. Above 105 ppm the nitrogen in the tissue remained fairly constant. Differences between experimental materials in nitrogen uptake, although statistically significant, were not clear-cut and a single curve for nitrogen is presented for the four experimental materials *(Figure 2)*. Uptake of P, Ca, and Mg followed a pattern similar to that of N with the uptake being low when nitrogen was low and

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[2]) Emission spectrographic techniques were used in determining P, K, Ca, and Mg. Nitrogen was determined using the standard Kjeldahl procedure.

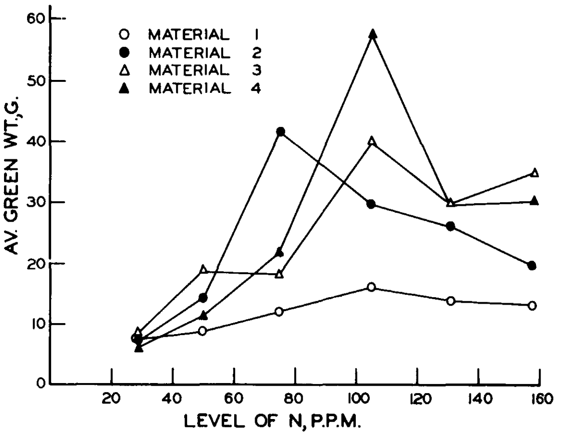

Fig. 1. — Differences in Average Green Weight of Trees Grown for Forty Days at Six Levels of Nitrogen.

Table 3. — Summary of analysis of variance "F" test values for differences between materials and treatments for green weight data.

Source of variation	D.F.	Significant "F" test values tabulated by expt. trials[1]		
		N	P	K
Materials (M)	3	10.1**	19.5**	22.9**
Treatments (T)	5	15.4**	12.6**	16.3**
M × T	15	3.1**	NS	3.1**

[1] A double asterisk indicates the "F" values were significant at the 1% level and the NS means the calculated "F" values were not significant.

increasing as nitrogen uptake increased. The same leveling-off trend at about 105 ppm is also evident. Only in the case of Ca and Mg were there well-defined differences between materials in the uptake and, as *Figures 3 and 4* illustrate, the native bigtooth aspen (Material 1) had the lowest uptake, and European gray poplar (Material 4) had the highest. The two hybrids were intermediate between the parent species.

Differences between experimental materials in the level of nitrogen in the tops, when nitrogen was in adequate supply (levels greater than 105 ppm), were not large. Average levels of N ranged from 4.00% for Material 3 to 4.3% for Material 2. The nitrogen levels, obtained under growth chamber conditions, are higher than leaf sample information reported for aspen growing on good sites in Minnesota [1.58% Voigt *et al.* (1957)], but was similar to levels reported by Bonner and Broadfoot [3.5 to 4.5% (1967)] and Hacskaylo and Vimmerstedt [2.9% (1967)] for cottonwood growing in sand culture system.

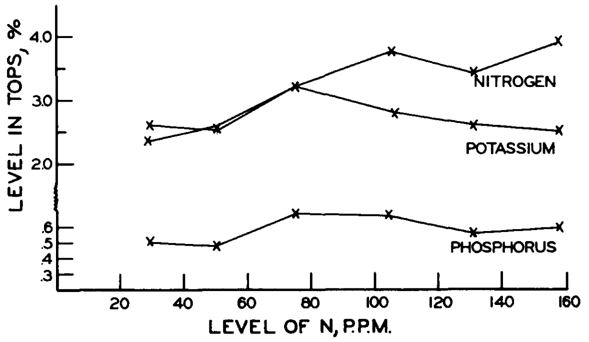

Fig. 2. — The Influence of Nitrogen Level on Nitrogen, Potassium, and Phosphorus Uptake. Data Plotted are Combined Values for the Four Types of Experimental Materials.

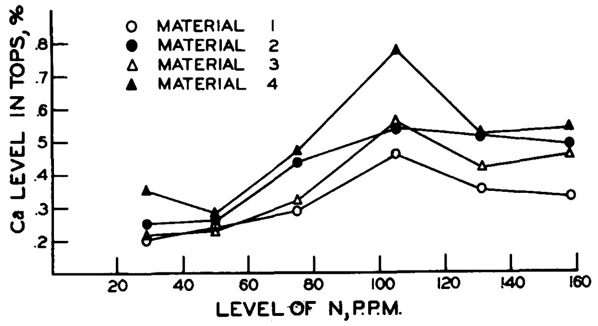

Figure 3. — The Influence of Level of Nitrogen in the Nutrient Solution on Uptake of Calcium. Differences Between Experimental Materials are Statistically Significant.

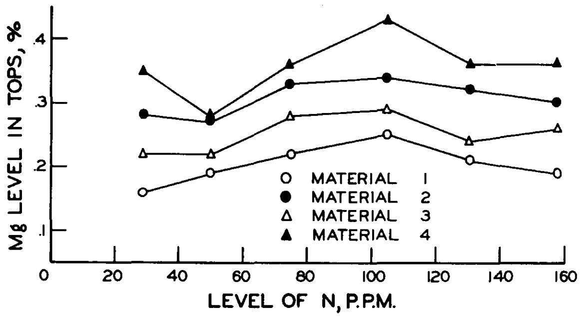

Figure 4. — The Influence of Level of Nitrogen in the Nutrient Solution on Uptake of Magnesium. Differences Between Experimental Materials are Statistically Significant.

Phosphorus Trial

The phosphorus trial was established using the same experimental procedures and the same test materials as were used in the nitrogen trial. Phosphorus levels were varied from 2 to 65 ppm (2, 11, 22, 43, 54, and 65 ppm) and the average total green weight (tops plus roots) was the measurement data selected to demonstrate growth response due to treatments. *Figure 5* summarizes the changes obtained in growth when the level of phosphorus was varied from 2 to 65 ppm.

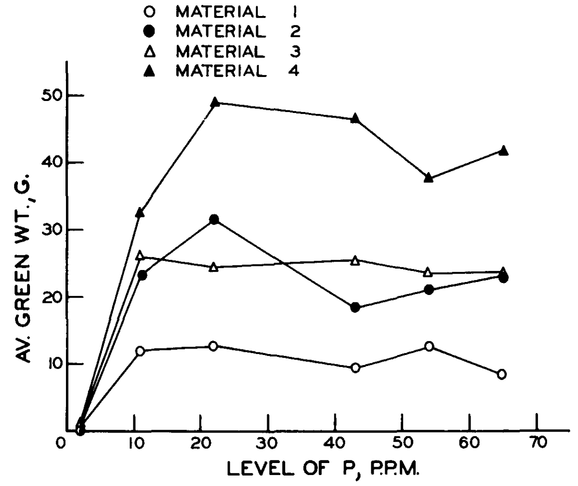

Figure 5. — Differences in Average Green Weight of Trees Grown for Forty Days at Six Levels of Phosphorus.

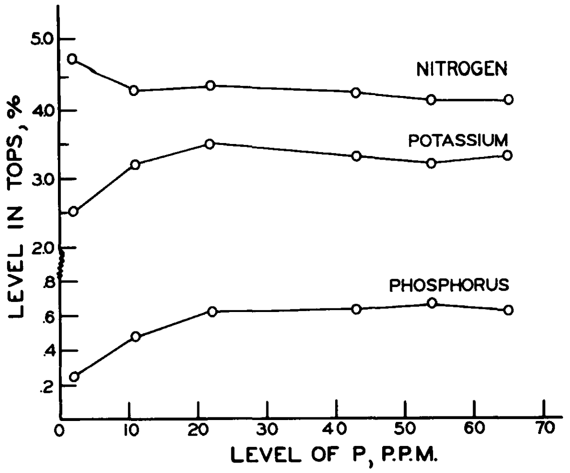

Figure 6. — The Influence of Level of Phosphorus on Uptake of Nitrogen, Potassium and Phosphorus. Levels Shown are Average Values for the Four Types of Experimental Materials.

Examination of the green weight data, using analysis of variance procedures, *(Table 3)* demonstrated that there were significant growth differences due to treatments and significant differences between the four types of experimental materials in their response to phosphorus treatments. All test materials grew very slowly at the 2 ppm level of phosphorus. Material 1, the bigtooth aspen cross, responded the least to increasing levels of phosphorus and Material 4 demonstrated the greatest response. Growth of the hybrids was intermediate between the two parent species and the growth curves of Materials 2 and 4 indicated slight decreases in growth resulting at treatment levels above 22 ppm.

Analysis of variance procedures were used to examine the results of the chemical determinations made on the tops of the trees. Statistical comparisons on the data indicate that increasing the level of phosphorus to 22 ppm resulted in significant increases in the level of P in the tops of the seedlings. Above 22 ppm the level in the tissue samples remained fairly constant. *Figure 6* illustrates the trends described and also demonstrates the influence that increasing the level of P had on P, N, and K uptake. There were no significant differences between materials in P, N, and K uptake. Nitrogen uptake was highest at the low levels of P while the K uptake curve was very similar to that of P.

The uptake of Ca and Mg was not affected by the phosphorus treatments and, as a result, no uptake curves are presented. There were, as in the nitrogen trial, significant differences between the four types of test materials in Ca and Mg uptake. The differences between materials followed a pattern essentially the same as shown in *Figures 3 and 4*. Uptake was the least for Material 1 and greatest for Material 4. The two hybrids (Materials 2 and 3) were intermediate.

The phosphorus levels reported are higher than given for mature leaf samples of aspen growing on good sites [0.16%, Voigt, *et al.* (1957)] and very similar to the values published for cottonwood grown in sand culture [0.5 to 0.7%, Bonner and Broadfoot (1967) and 0.8%, Hacskaylo and Vimmerstedt (1967)]. Early uptake and the immature nature of the growth chamber tissue samples are very likely major reasons for the nutrient level differences between field-grown and sand-culture-grown species of *Populus.*

Potassium Trial

Potassium levels were varied from 3 to 93 ppm (3, 15, 31, 62, 77, and 93 ppm) and the experimental design of the treatments was the same as described for previous trials. *Figure 7* illustrates response of the four test materials to increasing levels of potassium. When analysis of variance procedures were used, significant differences were obtained between test materials and between treatments for the illustrated green weight data *(Table 3)*. Growth was very slow at the low potassium levels and, although growth increases were obtained when the solutions contained up to 60 to 75 ppm, responses were not statistically significant above 31 ppm. The only exception was Material 4 which exhibited increased growth for K levels up to 62 ppm. Material 1 (bigtooth aspen) responded the least and Material 4 showed the greatest response to increasing levels of potassium.

Chemical analyses made on samples from the tops of the seedlings grown at the several levels of potassium were examined for differences between treatments and differences between test materials in nutrient uptake. Differences obtained between test materials in potassium uptake were not statistically significant. These data also indicate that varying the level of K had no influence on the uptake of N or Ca, but did affect the levels of P, K, and Mg in the tops of the seedlings (see *Figures 8 and 9*).

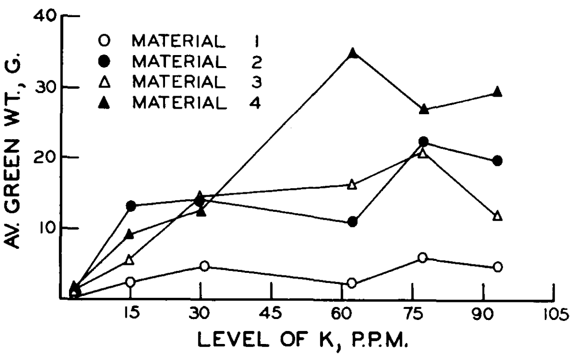

Figure 7. — Differences in Average Green Weight of Trees Grown for Forty Days at Six Levels of Potassium.

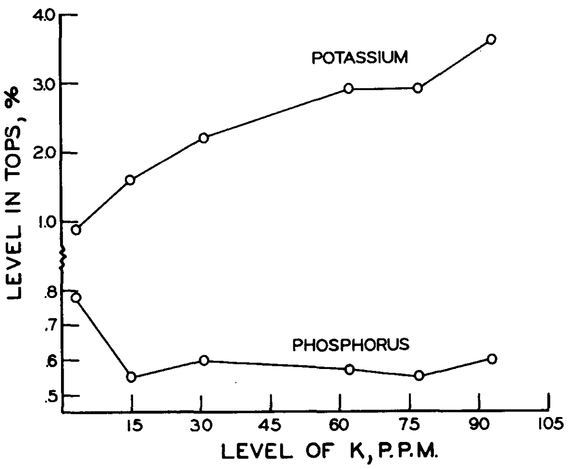

Figure 8. — The Influence of Level of Potassium on Uptake of Potassium and Phosphorus. Levels Shown are Average Values for the Four Types of Experimental Materials.

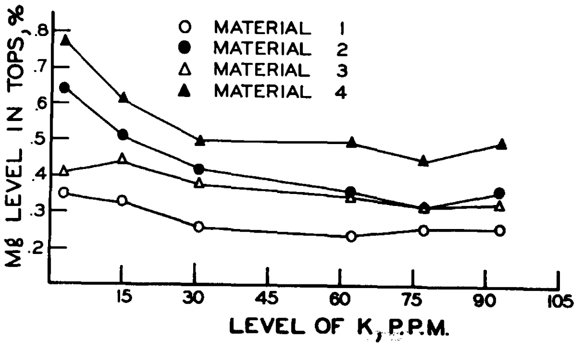

Figure 9. — The Influence of Level of Potassium in the Nutrient Solution on Uptake of Magnesium. Differences Between Experimental Materials are Statistically Significant.

Illustrated in *Figure 8* is the change in percent potassium which occurred with increasing K levels in the nutrient solution. Potassium tissue levels continued to increase well beyond the point where the treatment levels gave growth response. Uptake of P was high at the very lowest level of K (3 ppm) and dropped to a normal level at K levels above 15 ppm. Earlier workers dealing with deficiency symptoms in trees have suggested that low potassium results in high phosphorus concentration. The phosphorus in turn is believed to immobilize the iron in the plant and results in chlorotic leaves and reduced growth. The data obtained from the potassium growth chamber trials support the low K — high P theory.

Based upon growth response and nutrient uptake data, optimum levels of K in the nutrient solutions appeared to be 62 to 77 ppm. Average levels of K in the tissue, when growth was normal, varied from 2.8 to 3.1%. Growth of Materials 1, 2, and 3 increased only a minor amount when levels of potassium exceeded 31 ppm. Material 4 gave increased growth up to 62 ppm. The 2.8 to 3.1% potassium levels in the tissue are higher than reported for field-grown aspen [1.25%, Voigt, *et al.* (1957)] and similar to levels given for cottonwood [3.0—4.0%, Bonner and Broadfoot (1967, and 4.6%, Hacskaylo and Vimmerstedt (1967)] growing at adequate nutrient levels.

Considerable information exists regarding levels of potassium in tree leaves when potassium is in low supply. Generally, levels of 0.7 to 1.0% or less indicate K-deficient growing conditions. Sucoff and Perala (1965) reported 0.46—1.55% for young leaves and 0.20—0.70% for older leaves were indicative of potassium-deficient growing conditions for several species of hardwood. Walker (1955) found potassium levels in mature *Populus tremuloides* leaves were normally less than 0.7% for trees growing on potassium-deficient soil.

Related Observations

Growth Differences Between Experimental Materials: — The overall growth potential of the four types of experimental trees is of interest. One method of obtaining an estimate of the relative early growth of each material is to combine by test materials the growth data for all experimental trials. Growth differences at the higher nutrient levels provide a realistic picture of the early growth differences between test materials. Test Material 4 quite consistently had higher average green weights than Materials 2 and 3. Growth of Material 1 was much lower than the other three materials and responded very little to increasing nutrient levels. No evidence of hybrid vigor was exhibited by the two hybrids being tested.

Total Nutrient Uptake: —

Another use that was made of the available data was to look at the total or absolute uptake by the tops of the trees when nutrient levels were near optimum. For example, in the nitrogen experimental trial, best growth was obtained for Materials 1, 3, and 4 at the 105 ppm level of nitrogen and for Material 2 at 75 ppm. Using the dry weight of the tops and the level of the several elements in the tissue when growth conditions were optimum, estimates of the amount of each element removed from solutions were obtained. When these same procedures were repeated for each growth chamber run and the data averaged, the information in *Table 4* was obtained. Using such a procedure provides some indication regarding relative withdrawal rates when the various types of experimental materials are grown under near optimum conditions.

Statistical analyses of the data revealed that when the four types of materials were grown under optimum conditions for 40 days, Material 4 removed greater total amounts of nutrients from the solutions. Material 1 removed the least amount and the two hybrids were intermediate. The differences between materials in total uptake *(Table 4)* were highly significant for each of the elements listed and resulted from the combination of differences in growth and differences in the levels of the several elements in the plant tissue.

Discussion

One limitation of a sand culture system is that problems arise when the results are applied to natural soil systems. Also, the technique of holding all nutrient levels except one constant and varying this single element will give slightly different "optimum levels" than will be obtained using a well-designed factorial experiment.

Based upon the growth response curves and the nutrient uptake data, the aspen and aspen hybrid seedlings grew best at 75 to 100 ppm N, 22 ppm P, and 62 to 77 ppm K. Average levels of N, P, and K in the tops when growth was near optimum were 4.0 to 4.3% for nitrogen, 0.58 to 0.65% for phosphorus, and 2.8 to 3.0% for potassium. Nutrient levels found in the tops appear to be useful for comparisons with August-collected leaves of young aspen growing on sandy soils. Growth and nutrient requirements of aspen hybrids in relation to the parent species are of particular interest. The results suggest that the two hybrids will grow more rapidly and have higher soil fertility requirements than the native bigtooth aspen. It also appears that bigtooth aspen, which grows on well drained sandy soils, can be expected to show little response to fertilizer treatments. Comparisons made, taking into consideration both rate of growth and nutrient levels in the tops, indicate that young stands of European gray poplar could be expected to remove considerably larger amounts of N, P, K, Ca, and Mg from the soil than native bigtooth aspen. Fertilizer trials on sandy soils are being used to relate sand culture work to natural soil systems.

Table 4. — Nutrient uptake by tops at near optimum growing conditions.

Test material	Level of elements, g.				
	N	P	K	Ca	Mg
1	0.35	0.06	0.26	0.03	0.02
2	0.77	0.11	0.60	0.08	0.06
3	0.73	0.10	0.53	0.08	0.05
4	1.17	0.17	0.85	0.17	0.12

Summary

The growth and nutrient requirements of hybrids between European gray poplar (*Populus canescens* Sm.) and bigtooth aspen (*P. grandidentata* Michx.) were investigated by comparing the behavior of the two hybrid progeny groups with the performance of seedlings from the "parent species". Interrelated trials were conducted in which the influence of varying N, P, K, a single element at a time, was investigated. Analysis of measurement data revealed there were significant growth differences between the four types of experimental trees. Chemical determinations made on the tops of the trees demonstrated that there were significant between-material differences in the uptake of N, Ca, and Mg. Evidence was also obtained indicating the uptake of certain elements influenced the utilization of other major nutrients. Estimates made of the amounts of nutrients removed from the solutions by the tops revealed total uptake by the European gray poplar seedlings was approximately three times as great as that of the bigtooth aspen seedlings. Nutrient uptake by the hybrids was intermediate between the two parent species.

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Short Note

Systematic Lay-outs for Seed Orchards

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Since 1965 I have discussed the use of systematic lay-outs for seed orchards (Giertych 1965) with several people. The advantages of a systematic lay-out are readily admitted (inbreeding minimized, ease of locating ramets, possibility of extending the lay-out in all directions, and the independence of the lay-out on the size and shape of the orchard) but I have met three criticisms: 1^0 the system of Giertych (1965) is difficult to use, 2^0 seed orchards of more than 65 clones are frequently being established and 3^0 the progeny of such seed orchards will include a large number of full-sibs.

The first criticism has been most frequent but came as a surprise, since I felt that the method was much easier to employ than any other published thus far. The criticism means that in the description of the mathematics used to arrive at the lay-outs the simplicity of their practical use was lost. This is one point I hope to rectify in this note.

I have also prepared lay-outs for larger numbers of clones (*table 1*) to extend the practical use of the method. I have provided here only information about lay-outs for numbers of clones which give the optimum quadratic scatter of ramets. There is sufficient of these to choose from when planning any seed orchard and I recommend that these be used.

The third argument about the progeny containing too many full-sibs would become serious if we do collect seed from stands established from seed orchard seed. This could lead to inbreeding. However by the time forests established from seed produced in existing seed orchards themselves reach the age of seed production all our seed will be produced in seed orchards. Thus the danger of inbreeding in the second generation should not be exaggerated. Furthermore we can exploit the tendency in a seed orchard for a ramet to be pollinated primarily by its windward neighbour by selecting as neighbours those clones which in combination show specific combining ability. In the systematic lay-out I advocate each ramet of a clone has the same arrangement of neighbours around it and the possibility of using specific combining ability is thereby enhanced.

The computer programs for seed-orchard lay-outs proposed by la Bastide (1967) aim at avoiding repetition of neighbour combinations so as to increase the chances of panmixy. Additive gene effects will influence the progeny of the seed orchard whether there is panmixy or not. Any value or harm we might expect from specific combining ability will average out over the whole seed orchard crop to about the same extent whether we vary the composition of each group of clones or not. Also, as already mentioned above, if anything definite is known about specific combining ability between various clones we can exploit that knowledge by assigning appropriate locations to the clones.

Increasing the chances of panmixy appears to be the only merit of la Bastide's method over the systematic layout. His method is more cumbersome to use because a new lay-out must be calculated for each number of clones, each number of ramets and each shape of area and the calculations are very expensive of computer time. Moreover the lay-out does not allow for thinning in the seed orchards.