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EFFECTS OF POTASSIUM ON GROWTH AND WOOD ANATOMY OF A POPULUS HYBRID[1]

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ABSTRACT

The effects of five levels of potassium in nutrient solution on stem characteristics and wood anatomy were studied using hybrid poplar clone NE-49 (*Populus maximowiczii* × *P.* × *berolinensis* Dipp). Stems grown in 2 and 50 ppm K solutions were tallest and heaviest. Percentages of wood and pith seen in the cross section varied among treatments, but the percentage of bark remained the same. Regression equations were developed indicating relationships between cell dimensions and solution potassium level. Both vessel element and fiber lengths and diameters were affected by potassium levels as was vessel element cell-wall thickness. Fiber cell-wall thickness was not influenced by the treatment.

Keywords: Hybrid poplar, potassium, specific gravity, cell length, fiber length, fiber width, fiber wall thickness, vessel element length, vessel element width, vessel element thickness, tissue volumes, foliar analyses.

INTRODUCTION

Applications of fertilizers may be needed to achieve optimum production of genetically improved tree varieties. For several species, including some improved varieties of *Populus*, near-optimum nutrient levels for volume production have been determined (Einsphar 1971). Less is known, however, on the effect of nutrient differences on wood properties.

Foulger and Hacskaylo (1968) found that seedlings of *Populus deltoides* Barter., when deprived of potassium, grew shorter, narrower fibers and narrower annual rings in their lower stems, and narrower vessel elements in their upper stems than did controls. Foulger et al. (1971) studied the interaction of five basic nutrients within the same species. They found fiber length maximum when nutrients included about 17 ppm N and 53.1 ppm K, but other relationships were not clearly established. They concluded that more basic information on specific effects of nutrients on wood anatomy would be required. (Foulger et al. 1972)

In the present study we observed growth and wood anatomy in a single hybrid clone, NE-49 (*Populus maximowczii* × *P.* × *berolinensis* Dipp; Stout and Schreiner 1933; Wendel 1972) as affected by concentration of K in nutrient solution. Use of material reproduced vegetatively from a single clone should minimize variation because of genetic differences between trees, thus maximizing sensitivity to applied treatments.

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EXPERIMENTAL

Growth of cuttings

The experiment was completely randomized and designed to compare the effects on growth and wood characteristics of cuttings grown in nutrient solutions containing five levels of potassium: 2, 10, 50, 100, and 150 ppm. The remaining composition of the nutrient solutions was 6 ppm NH_4-N; 140 ppm NO_3-N; 16 ppm P; 200 ppm Ca; 24 ppm Mg; 0.5 ppm B; 0.5 ppm Mn; 0.05 ppm Zn; 0.02 ppm Cu; 0.01 ppm Mo; and 1 ppm chelated Fe.

After two weeks' storage at −10 C, and top dipping in paraffin to minimize moisture loss, 50 NE-49 cuttings, each 20 cm long, were weighed and set in polyvinyl chloride (PVC) pellets. Preliminary studies had shown that mechanical aeration was not necessary when the PVC pellets, which were an assortment of shapes and sizes, were used.

Two cuttings were set in each of twenty-five 22-cm-diameter containers, which were randomly assigned a treatment (K level solution, supplied by an individual 8 liter reservoir) and a permanent greenhouse location. They were irrigated with glass-distilled deionized water for two weeks, then with dilute nutrient solutions for one week. The pots and nutrient reservoirs were then flushed with distilled deionized water after which appropriate nutrient solutions, identical except for K-level, were added to the reservoirs. Thereafter the pots and the reservoirs were drained every two weeks, flushed with distilled deionized water, and drained prior to adding new solutions. Height growth was measured weekly.

January daylight was supplemented by burning a combination of fluorescent and incandescent bulbs 14 hours daily, providing 0.05 g-cal/cm^2/min of supplemental light. After 14 weeks, the plants were receiving a maximum total light energy of 0.51 g-cal/cm^2/min (ca 3400 ft.-c) (Reifsnyder and Lull 1965).

Measurements

After the 14-week growing period, we separated new growth from each original cutting and measured and weighed it before dividing a portion of the new shoot into sample segments according to the scheme in Fig. 1. Segments B, C, and D we promptly immersed in distilled water preparatory to subsequent analysis. Foliage from each sprout was dried at 60 C and ground to pass through a 40-mesh screen in a Wiley mill.

We determined levels of P, K, Ca, Mg, Mn, and Fe in the foliage by standard emission spectrometric techniques described by Baker et al. (1964); nitrogen determinations were by the Kjeldahl method.

Stem segment D was debarked, depithed, and macerated by Burkart's (1966) technique. The macerations were mounted in glycerin jelly on glass and cell lengths were measured with a light microscope equipped with a filar micrometer. Ten cells of each cell type were measured from each stem. Preliminary work had shown that 10 measurements per stem of the cell sizes found here were enough to provide statistically valid numbers. Stem segment E was reserved for use in another study.

Stem segment C was embedded in celloidin and sectioned (Sass 1958). Diameter of the stem outside bark (DOB), diameter inside bark (DIB), and diameter of the pith (DPith), were each measured twice, at right angles, with a filar-micrometer-equipped light microscope. Proportion of bark, wood, and pith were calculated as percentages of total cross-sectional area.

Fiber and vessel element width (tangential direction) and double cell-wall thicknesses were measured with a polarizing light microscope equipped with a filar micrometer on 20-μm-thick cross sections cut from the embedded samples. Each measurement was repeated 10 times on each stem.

The number of rays on each cross section was counted with the microscope. Ray spacing (number of rays per millimeter at the cambium) was computed by dividing

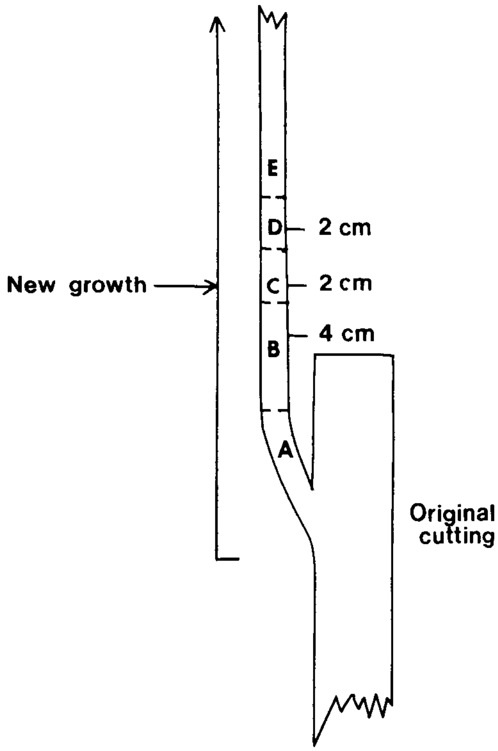

FIG. 1. Schematic diagram showing allocation of specimens from the new growth. Segment A was discarded to eliminate butt swell effects. Segment B was used for specific gravity; C, for light microscope studies; D, for macerations; and E preserved for future study.

the number of rays per stem by the calculated circumference.

Stem segment B we used to determine gross specific gravity by two methods: pycnometric (SG_{pyc}) (Stamm 1964) and maximum moisture content (SG_{mmc}) (Smith 1954). In the calculation of SG_{mmc}, the density of wood substance was assumed to be 1.53 g/cc. The density of wood substance (ρ_{ws}) was also measured pycnometrically in water (Stamm 1964) using wood meal from the gross specific gravity samples passing a 40-mesh and retained on an 80-mesh screen.

Mortality

All 50 of the cuttings initially rooted and produced new growth. However, 11 either died during the study or were discarded because of mechanical failures, leaving 39 stems available for measurement and analysis. Statistical analyses thus required solutions applicable to unequal sample sizes.

Analysis of mortality showed no indication of a relationship between potassium level and number of surviving cuttings.

RESULTS AND DISCUSSION

Foliage analyses

Levels of N, P, Ca, Mg, Mn, and Fe in the foliage (Table 1) were within ranges considered adequate for plant growth (Hacskaylo and Vimmerstedt 1967), except for the low P level, 0.29%, for plants in the 10 ppm K level treatment. This latter value for P could have influenced some of the measured variables, but we consider it improbable.

Foliage K was highest (1.28% and 1.30%) for plants grown in solutions with 50 and 100 ppm K, and lowest (0.68% and 0.77%) for those in 2 and 10 ppm K solutions. Plants grown in the 150 ppm solution had an intermediate K level (1.20%). The two lower values are below the level considered

TABLE 1. *Mean mineral content of foliage of test cuttings, by K content of nutrient solution*[a]

Solution	N	P	K	Ca	Mg	Mn	Fe
	(% oven-dry weight)					(ppm)	
2 ppm K	3.22 A	0.41 A	0.68 A	3.58 BC	0.53	147 B	178 A
10 ppm K	2.92 A	0.29 A	0.77 A	3.91 AB	0.44 A	156 AB	164 A
50 ppm K	3.68 A	0.62	1.28 B	4.72 A	0.46 A	183 A	196 A
100 ppm K	3.28 A	1.07	1.30 B	2.91 BC	0.36 AB	186 A	196 A
150 ppm K	3.27 A	0.88	1.20	2.74 C	0.32 B	227	208 A

[a] Within each column, means followed by the same capital letter are not significantly different at the 0.05 probability level.

TABLE 2. *Mean stem parameter values, by K content of nutrient solution*[a]

Solution	Stem: Height (cm)	Stem: Weight (g)	Stem diameter: DOB	Stem diameter: DIB (mm)	Stem diameter: DPith	Area: Bark	Area: Wood (%)[b]	Area: Pith
2 ppm K	75.3 A	8.99 A	4.07 A	2.99 A	0.91 A	45.6 A	49.2 AB	5.1 BC
10 ppm K	58.3 AB	6.87 AB	3.69 AB	2.77 AB	0.91 A	43.0 A	50.1 A	6.6 AB
50 ppm K	71.6 A	7.67 AB	3.94 A	3.03 A	0.77 B	40.8 A	55.2 A	3.9 C
100 ppm K	44.1 BC	4.18 BC	3.27 BC	2.41 B	0.82 AB	44.5 A	49.1 AB	6.2 ABC
150 ppm K	33.8 C	2.48 C	2.95 C	1.93	0.85 AB	49.7 A	41.5	8.6 A

[a] Within each column, means followed by the same capital letter are not significantly different at the 0.05 probability level.
[b] Analysis on data transposed to $\sqrt{}$ arc sine (Steel and Torrie 1960).

necessary for plant growth by Hacskaylo and Vimmerstedt (1967); the highest ones are also below levels (3.0+%) reported as optimum by these authors and by Bonner and Broadfoot (1967).

Gross stem parameters

Mean stem heights, weights, and diameters with and without bark, (Table 2) did not differ significantly among plants grown in the three lower K-level solutions, and in most cases were significantly larger than for plants from the two higher level solutions. This indication of an inhibiting effect from the 100 and 150 ppm K solutions is confirmed by lower height growth (Fig. 2) for both these solutions, and the abrupt termination of height growth of the seedlings in 150 ppm K solution after 6 weeks. Seedlings in the latter solution set terminal buds shortly thereafter.

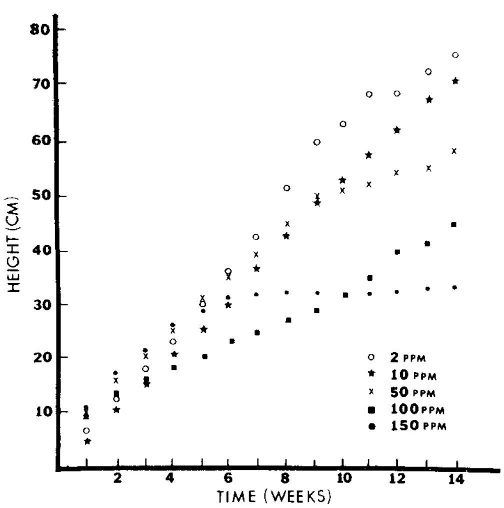

FIG. 2. Cumulative height growth by treatments.

Differences in pith diameter were not significant for the three strongest solutions, and values for neither of the two stronger solutions varied significantly from either of the two weakest. We conclude that pith diameter was little affected by K-level of nutrient solution. Likewise, proportions of cross sections in bark, wood, and pith show little correlation with K-level. Murphey et al. (1962) reported lower proportions of phloem in *Liquidambar styraciflua* seedlings grown in potassium-deficient solutions.

Specific gravity

Mean specific gravity of the stem, 0.331, and of the wood, 0.363, (Table 3) are in line with values reported by Cech et al. (1960) for one-year-old wood of *Populus trichocarpa* Torr. & Gray.

The highest stem specific gravity was 0.373 for the 2 ppm K material which was significantly greater than the specific gravities of the 10 and 150 ppm K stems. Values for the latter stems were significantly less than all other values.

A similar trend was in evidence for the wood specific gravity means. The highest mean, 0.392, for wood from the 2 ppm K solution, was not statistically different from the means for the 10 and 50 ppm K wood. However, the 10, 50, 100, and 150 ppm K wood means were also grouped.

Murphey and McAdoo (1969) and Mur-

TABLE 3. *Mean stem and wood specific gravity values by K content of nutrient solution and method of determination*[a]

Treatment	Stem	Wood
Solution K-level		
2 ppm K	0.373 A	0.392 A
10 ppm K	0.328 B	0.364 AB
50 ppm K	0.344 AB	0.371 AB
100 ppm K	0.341 AB	0.356 B
150 ppm K	0.270	0.336 B
Method of Determination		
Maximum moisture content	0.324 A	0.358 A
Pycnometric	0.338 A	0.369 A
Interaction	N.S.[b]	N.S.

[a] Those means followed by the same capital letter are not significantly different at the 0.05 probability level.
[b] *Nonsignificant.*

phey et al. (1969) found similar trends toward high specific gravity in seedlings of *Robinia pseudoacacia* L. and *Larix occidentalis* Nutt. grown in solutions deficient in potassium. Determining the specific gravity of each sample by the two techniques provided an indirect evaluation of the chemical composition of the material. The underlying assumption in the maximum moisture content method is that the ρ_{ws} measured in water is between 1.53 and 1.55 g/cc. If the assumption of 1.53 made in this study was incorrect, one would have expected this to be reflected in differences between SG_{Pyc} and SG_{mmc}, assuming the former value to be the correct one. Analysis of variance indicated that there was no significant difference in specific gravity because of the method of determination for either the wood or the stems. The experimentally determined ρ_{ws} for the combined treatments was 1.548 g/cc (Table 4). Stamm (1964) indicated that the ρ_{ws} determined in water ranged from 1.506 to 1.548 g/cc for wood meal of several species. Kellogg and Wangaard (1969) found that extractive-free *Populus deltoides* sapwood wafers had a ρ_{ws} of 1.528 g/cc.

TABLE 4. *Mean density of wood substance values (g/cc), by K content of nutrient solutions*[a]

Solution	Mean	σ
2 ppm K	1.642 A	0.026
10 ppm K	1.396	0.012
50 ppm K	1.532 A	0.062
100 ppm K	1.608 A	0.071
150 ppm K	1.562 A	0.099

[a] Those means followed by the same capital letter are not significantly different at the 0.05 probability level.

Among the five treatments, only the 10 ppm K wood meal had a significantly lower density than the mean. This could indicate that the wood substance of the 10 ppm K samples contains considerably less cellulose (density 1.55 to 1.58 g/cc in water) and more lighter material such as lignin and hemicelluloses. Since there are no evident trends in the data, and the single significant deviation is not associated with either extreme of the treatments, we doubt that there is such a chemical difference, and feel that availability of potassium has little effect on wood substance density in this hybrid clone.

Anatomical features

Table 5 summarizes the results of the statistical analyses of values for anatomical characteristics. Means for all characteristics

TABLE 5. *Dimensions of fibers and vessel elements, and ray spacing, by K content of nutrient solution*[a]

	Vessel element			Fiber			
Solution	Length (mm)	Diameter (μm)	Double Cell-Wall thickness (μm)	Length (mm)	Diameter (μm)	Double Cell-Wall thickness (μm)	Ray spacing (number per mm)
2 ppm K	0.247 B	32.6 B	2.9	0.449 A C	10.9 A	3.3 A	14.0 A
10 ppm K	0.246 B	30.5 A	3.4 A	0.464 BC	10.2 B	3.5 A	13.7 A
50 ppm K	0.221 A	33.5 B	3.5 A	0.475 B	10.7 A	3.3 A	13.3 A
100 ppm K	0.232 A	29.5 A	3.7	0.430 A	10.1 B	3.4 A	11.0
150 ppm K	0.235 AB	29.5 A	3.2	0.389	10.4 AB	3.5 A	13.9 A

[a] Within each column, means followed by the same capital letter are not significantly different at the 0.05 probability level.

TABLE 6. *Anatomical characteristics as functions of solution potassium level*

Equation no.		R or r	Sy/x
(1)	Vessel element length (μm) = 248 − 0.548 (K) + 0.003 (K^2)	0.45	17.6
(2)	Vessel element diameter (μm) = 32.01 − 0.0176 (K)	−0.32	2.83
(3)	Vessel element double cell-wall thickness (μm) = 3.07 + 0.0157 (K) − 0.0001 (K^2)	0.57*	0.34
(4)	Fiber length (μm) = 456 + 0.485 (K) − 0.006 (K^2)	0.65*	32.6
(5)	Ray spacing (#/mm) = 13.92 − 0.0387 (K) + 0.0000016 (K^2)	0.48*	1.65

* Indicates significant at the 0.05 probability level.

except double cell-wall thickness of fibers varied significantly with K level of the growing medium, but in rather inconsistent patterns. For both vessel elements and fibers, largest dimensions tended to be associated with less concentrated solutions, although vessel element diameter and fiber length were largest for the 50 ppm solution, and fiber diameter for the 10 ppm solution ranked with the lowest. The only significant variation in ray spacing was for the 100 ppm solution, whose mean (11.0) was lowest of the five.

These somewhat erratic patterns of variation are in general agreement with the patterns shown by gross stem measurements (Table 3), which tended towards larger values for the solutions with lower K levels.

Because the relationship, if any, between the anatomical data and the solution K level appeared to be complex, equations were developed to determine the mathematical relationships between these data. Best significant predicting equations are presented in Table 6.

Equation 1 indicates that minimum vessel element lengths would be found when solutions contained 90 ppm K. Vessel element diameter (Equation 2) was best related to the potassium level in the nutrient solution by a simple linear expression. The correlation coefficient, r, for this equation was barely significant at the 0.05 probability level. Equations 3 and 4 are curvilinear, and indicate that the thickest cell walls and the longest fibers should be found in solutions containing 78 and 40 to 41 ppm K, respectively. Foulger et al. (1971) indicated that optimum solution levels of N and K for maximum fiber length in *Populus deltoides* would be 17 ppm N and 53 ppm K, the latter being in fairly close agreement with Equation 4.

The maximum predicted fiber length, 0.466 mm, for the NE-49 data in this research, and that for *Populus deltoides* found by Foulger et al. (1971), 0.55 mm, are comparable to fiber lengths for *Populus* spp. grown in field studies. Kennedy and Smith (1959) found that fiber length ranged from 0.47 to 0.55 mm for one-year-old stump sprouts while Cech et al. (1960) reported lengths of 0.45 to 0.81 mm.

One of the major functions of rays is to provide the cambial initials with carbohydrates and nutrients. Ziegler (1964) suggests that this function may be the effective mechanism for controlling ray spacing, since when initials are too far from the nutrient sink, the initials either die or form new ray initials.

Murphey et al. (1969) found that low potassium solution levels decreased the ray index or spacing significantly when compared to that for cuttings grown in full-strength solution. Foulger et al. (1971) found no clear-cut relationship between nutrient levels in solution and the amount of cross-sectional area occupied by the rays.

Equation 5 indicates that a minimum number of rays per millimeter or the maximum ray spacing should occur around the 90 ppm potassium level, suggesting that to be the optimum level for cambial activity and cell production from the standpoint of mineral nutrition.

SUMMARY

The highest level of potassium tested, 150 ppm, was clearly detrimental to growth of the plants and quality of the resulting wood. Those plants growing in the high solution ceased elongation during the sixth week of the study and set terminal buds. While mineral nutrient deficiencies have been related to growth cessation, potassium overabundance had not previously been shown to be a causal agent.

While the percentages of both wood and pith as seen in the cross-section varied significantly among treatments, the percentage of bark was statistically the same among the treatments. This suggests that the rates of xylem and phloem cell production were differentially affected by the treatments.

Gross growth in height and weight averaged highest in solutions with 2 to 50 ppm K. Anatomical development peaked, however, at higher concentrations. Equations predict maximum fiber length at 40 ppm K, minimum vessel element length at 90 ppm K, maximum vessel cell-wall thickness at 78 ppm K, maximum ray spacing at 90 ppm K. None of the anatomical dimensions were at maximum or minimum at either of the solution extremes—2 and 150 ppm K.

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