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Nutrient Element Balance: Response of Tung Trees Grown in Sand Culture to Potassium, Magnesium, Calcium, and Their Interactions¹

By C. B. SHEAR, plant physiologist, H. L. CRANE. principal horticulturist, and A. T. MYERS, formerly associate biochemist. Division of Fruit and Nut Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration²

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²George F. Potter advised and assisted in the statistical analyses and interpretation of the data presented in this bulletin.

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INTRODUCTION

The culture of tung (Aleurites fordii Hemsl.) in the United States is restricted by climatic requirement to the Coastal Plain of the Southeastern States. Much of this region is characterized by sandy, waterdeposited soils of low base-exchange capacity that are subjected to extensive leaching by heavy rainfall. Consequently, many of these soils are low in plant nutrients, especially certain of the heavy metals, or the so-called minor elements. Because of these conditions and because the tung tree has a high mineral-nutrient requirement, it was expected that nutritional problems would be a major factor in tung production. Experience has borne out this expectation.

It was realized that any research program which was to serve adequately the developing tung industry must include studies to determine efficient and reliable means of diagnosing and correcting unbalanced nutritional conditions. Though knowledge of nutritional requirements is to be applied to plants grown in soil, it is believed that the fundamental information can be obtained most readily by solution or sand cultures wherein careful control of the plant nutrients can be maintained. Sand-culture studies, therefore, were included among the first projects started when the Department of Agriculture inaugurated research on tung in 1938. As facilities were not available at tung laboratorics established in the South, this work was carried out in a greenhouse at the Plant Industry Station, Beltsville, Md.

The principal objectives of these studies have been:

- 1. To determine the effects of varying levels of supply of individual nutrient ions and varying combinations of levels of a number of ions on plant growth and the symptoms of nutritional disorder expressed.
- 2. To determine the relations between nutrient supply and mineral composition of leaves.
- 3. To attempt to correlate plant growth or the symptoms of unbalanced nutrition with leaf composition.

This bulletin presents the results of a sand-culture experiment carried out during the growing season of 1945. The experiment was designed to determine the effects of varying ratios of calcium, magnesium, and potassium in the nutrient supply on plant growth and leaf composition.

The interactions that occur between the cations--criticium, magnesium, and potassium--with respect to their effects on the growth of plants and on the absorption and accumulation of each by the plant have received

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NUTRIENT ELEMENT BALANCE IN TUNG TREES

the attention of numerous investigators. There is still, however, much apparent disagreement among the various workers in the field of both plant physiology and soil chemistry regarding the behavior of these elements. In order to establish fundamental principles and to clarify the widely accepted use of foliar analysis as a means of determining the nutritional status and fertilizer requirements of crops, it is important that a better understanding of the relationships between these, as well as the other nutrient elements, be gained.

MATERIALS AND METHODS

SOURCE OF PLANT MATERIAL

In these experiments seedling plants were used that were grown from the seeds of a single, open-pollinated tree designated as Florida 551. In the absence of established clonal varieties of tung at the time this experiment was undertaken, such a procedure was considered the most satisfactory means of obtaining relatively uniform trees.

The seeds were soaked in a 1-percent solution of Morpholine for 48 hours, in order to attain faster and more uniform germi-ztion (25),³ and planted in quartz sand covered with sphagnum moss in a greenhouse bed at Beltsville, Md., March 2, 1945.

Tung seedlings, after producing four or five leaves, go into a period of apparent inactivity resembling rest, which lasts about 6 weeks. During this period there is practically no growth. The seedlings were allowed to go through this period before being transplanted into crocks containing sand preparatory to beginning differential nutritional treatment.

SAND-CULTURE METHODS

The sand-culture technique was employed in these experiments, because the conditions provided by such a medium more nearly approximate those of the soil than do those presented by the solution-culture methods. The requirements of the tung tree for physical support also made solution culture impracticable.

Many of the variations of the sand-culture method used and described have been concerned primarily with different means of supplying the nutrient solution. Each variation is credited with certain merits that recommend it for use with a particular plant or for the solution of certain types of nutritional problems. A study of the literature, however, shows that insufficient consideration has been given to the physical characteristics of the sand used. This is particularly unfortunate, as the airholding capacity and permeability of the sand used are often limiting factors in the absorption of nutrients and in the growth of many plants that are particularly sensitive to conditions of poor aeration in the substrate.

Preliminary experiments with tung trees in sand culture using Berkeley Springs No. 1 glass sand produced trees showing severe symptoms of poor aeration. Therefore, it scemed advisable to compare the physical properties of three of the grades of sand available from a commercial company in an altempt to find a suitable medium for use in future work.

^a Italic numbers in parentheses refer to Literature Cited, p. 50.

National Bureau	Percentage of sand retained on sieve of-								
of Standards sieve No.	8-mesh grade	F grade	No. 1 grade						
	Percent	Percent	Percent						
6	0	0	0						
2	.4	0	Ō						
(0	75.4	6.0	0						
Ŋ	22.0	37.2	.4						
U	1.6	30.6	9.2						
0	.4	15.8	40.4						
0	. 2	5.2	32.2						
Ø	0	2.4	12.4						
	0	1.2	4.0						
U	0	.6	1.0						
υ.,	0	.4	.2						
un,.	0	.6	.2						
Total.	100.0	100.0	100.0						

 TABLE 1.—Percentage of sand of various particle sizes in 3 commercial grades of Berkeley Springs glass sand

The data in table 1 show the differences in the percentages of the different particle sizes in the three sands examined. Data on the permeability of the same sands under a number of different conditions of moisture (table 2), the percentage of moisture at saturation, and the volume of air held in 33 pounds of each sand at saturation in 3-gallon glazed crocks (table 3) were obtained.

From these data it seemed probable that the No. 1 sand has an airholding capacity and permeability too low to provide an adequate oxygen supply and an exchange of atmosphere rapid enough to support

TABLE	2.—Permeability	oſ	\mathcal{S}	grades	oſ	Berkeley	Springs	glass	sand'
	under	diff	er	ent moi	stw	re conditio	ns	.,	

	Permeability of sand ¹								
Condition of sand	8-mesh grade	F grade	No. 1 grade						
Dry. -percent moisture. Saturated.	2,450 2,450 38	492 1,060 0	163 358 0						
For 15 minutes.	75 112 142	0	0						
For 20 minutes. For 30 minutes.	193 219	0 2 2	0 0 2						

¹ Expressed as cubic contineters of air passing per minute through a specimen of 1 cc. in volume under a pressure of 1 gm, per square continueter.

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TABLE 3.—Percentage of moisture at saturation¹ and volume of air in saturated sand in S-gallon glazed crocks containing the indicated quantities and grades of sand and with drainage holes covered with the indicated materials

Grade of sand and quantity	Material covering drainage hole	Moisture at saturation	Volume of air per crock of saturated sand
		Percent	Cc.
No. 1, 33 lb	Mineral wool	26.7	100
No. 1, 25 lb	Screen ² + 10 lb. pea gravel.	21.1	100
F, 31 lb	Screen ² + 2 lb. 8- mesh sand.	13.3	1,600
8-mesh, 33 lb	Serven ²	9.4	2,675

¹ The moisture content of the sand was brought to saturation by adding water while stirring; expressed as grams (percent) of water per EM gm. of dry sand.

⁴ 16-mesh bronze wire screen, coated with one coat of red lead paint and two coats of asphalt varnish.

normal plant growth, especially for plants having a high rate of root respiration.

The 8-mesh sand provided the opposite conditions of air-holding capacity and permeability, having such a high air-holding capacity and permeability as to preclude the maintenance of an adequate moisture supply for normal plant growth. The characteristics of the F-grade sand were found to be intermediate between those of the No. 1 and 8-mesh sands.

In addition to the study of the physical properties of these sands, an experiment was also carried out to determine the response of tung seedlings under identical nutritional conditions to the three grades of sand in crocks provided with different means of covering the drainage holes. The results were such as would be expected on the basis of the previously obtained information. No. 1 sand provided inadequate aeration, regardless of the attempted improvements in drainage, and the 8-mesh sand was incapable of holding sufficient moisture to provide for the requirements of the trees without too frequent application of solutions. The F-grade sand, though having only a 13.3-percent moisture-holding capacity at saturation as compared to 26.7-percent for the No. 1 sand, permitted the retention of 1,600 cc. of air per 31 pounds of F sand and 2 pounds of 8-mesh sand at saturation as compared with only 100 cc. per 33 pounds for the No. 1 sand. Nevertheless, the moisture-holding capacity of the F sand was adequate to supply moisture to even large tung trees (4 to 6 feet tall) when supplied with 1,800 ml, of nutrient solution every other day. At the same time, however, its air-holding capacity and permeability were sufficient to afford adequate initial aeration and rapid enough atmospheric exchange to produce normal root development and prevent the appearance of symptoms of poor aeration on the leaves or roots.

On the basis of this information the following procedure was used in the experiments herein reported.

The plants were grown in 3-gallon glazed crocks, each equipped with a side drainage hole three-quarters of an inch in diameter. The drainage hole was covered with 16-mesh bronze wire screen coated with one coat of red lead paint and two coats of asphalt varnish. In subsequent experiments, plastic screen has been used. Over this screen was placed 2 pounds of Berkeley Springs 8-mesh glass sand. Seedlings were carefully selected for uniformity, removed from the sand in which the seed had been germinated, and, after rinsing the roots with tapwater, were held in place in the crocks while 31 pounds of Berkeley Springs F-grade sand was poured around the roots. The sand was immediately saturated with tapwater. The date of transplanting was April 16, 1945. The transplanted plants were supplied with tapwater until their roots became reestablished, and then differential solution applications were given.

Nutrient solutions were applied by hand at the rate of 1,800 ml. per application. Applications were made twice a week while the plants were small (from May 1 to July 3, 1945), and three times a week from July 3 to September 7. From September 7 until the plants were harvested (September 17 to 24) tapwater was applied as needed to prevent wilting.

SOLUTION COMPOSITION

The formulation of nutrient solutions having a number of combinations of levels of the ions to be studied is complicated by variations in the concentrations of other ions that it would be desirable to hold constant. The use of base-exchange materials as carriers of the various ions is the only method so far devised to overcome this difficulty. The cost of such materials is prohibitive, however, in a study of the scope of the one reported.

After careful consideration, it was decided that the most feasible means was to allow the sodium, chlorine, and sulfate ions to vary within limits shown by previous experiments to be below the toxic level for tung. Subsequent experiments were carried out to determine the effect of these three ions on growth and leaf composition. The results showed that no significant differences in growth responses of tung resulted from variations in sodium, chlorine, or sulfur content in the solution when sulfur was adequately supplied and chlorine was kept below the toxic level. Previous experiments by the authors had shown that the chlorine content of the leaf tissue of tung was directly correlated with the chlorine content of the nutrient solution. Wide variations in available sodium in the solution was not correlated with the sodium content of the leaves. Because it has been shown (10) that chlorine and sulfate exert a competitive effect on one another, the ratio of these two ions was kept as nearly constant as possible.

The concentrations of the nutrient ions in the solutions used in the experiment (table 4) were based on the results of preliminary experiments with tung that had indicated the approximate levels for deficiency, optimum growth, and "luxary consumption." In all earlier experiments it was found that when nitrogen was supplied entirely as the nitrate ion, control of the pH of the cultures between solution applications was impossible. Neither was it possible to grow plants entirely free from symptoms of iron deficiency. In order to overcome these difficulties, one-fourth of the nitrogen was derived from the ammonium ion and three-fourths

NUTRIENT ELEMENT BALANCE IN TUNG TREES

TABLE	4 Concentration	0] 10NS-	in the	nutrient	solutions	for	the
		various tr	reatmen	ts			
Turet	Components	Fi Millieguiv	valents pe	er liter of jo	as in solutio	n	

Treat-	Cor	npon	ents	Milliequivalents per liter of ions in solution										
No.	к	Mg	Ca	ĸ	Mg	Са	N 2	PO4	SO13	Na	CI			
1 2 3	1 1 1	1 1 1	1 2 3	0.20 .20 .20	$0.20 \\ .20 \\ .20 \\ .20$	$0.60 \\ 3.60 \\ 10.80$	$11.56 \\ 11.56 \\ 11.56 \\ 11.56$	1.74 1.74 1.74	$2.22 \\ 2.22 \\ 4.37$	7.38 4.38 .77	0.30 .30 1.72			
4 5 6	1 1 1	2 2 2	1 2 3	.20 ,20 .20	$1.22 \\ 1.22 \\ 1.22 \\ 1.22$.60 3.60 10.80	$ \begin{array}{r} 11.56 \\ 11.56 \\ 11.56 \\ 11.56 \end{array} $	$\begin{array}{c} 1.74 \\ 1.74 \\ 1.74 \\ 1.74 \end{array}$	$2.42 \\ 2.42 \\ 5.40$	6.53 3.56 .77	.30 .30 1.72			
7 8 9] 1 1	333	1 2 3	.20 .20 .20	$3.67 \\ 3.67 \\ 3.67 \\ 3.67$.60 3.60 10.80	$11.56 \\ 11.56 \\ 11.56 \\ 11.56$	1.74 1.74 1.74	$2.42 \\ 2.42 \\ 6.61$	3.91 .91 .77	.30 .30 2.80			
10 11 12	$\frac{2}{2}$	1 1 1	$\begin{array}{c} 1 \\ 2 \\ 3 \end{array}$	1.22 1.22 1.22 1.22	.20 .20 .20	.60 3.60 10.80	$11.56 \\ 11.56 \\ 11.56 \\ 11.56$	1.74 1.74 1.74	2.22 2.22 4.96	6.36 3.32 .77	$.30 \\ .30 \\ 2.16$			
13., 14 15	2 2 2	2 2 2	1 2 3	$1.22 \\ 1.22 \\ 1.22 \\ 1.22$	$1.22 \\ 1.22 \\ 1.22 \\ 1.22$.60 3.60 10.80	11.56 11.56 11.56	1.74 1.74 1.74	2.22 2.22 5.74	$5.34 \\ 2.35 \\ .77$	$.30 \\ .30 \\ 2.41$			
16 17 18	2 2 2	3	$\begin{array}{c} 1 \\ 2 \\ 3 \end{array}$	$1.22 \\ 1.22 \\ 1.22 \\ 1.22$	$3.67 \\ 3.67 \\ 3.67 \\ 3.67$.60 3.60 10.80	11.56 11.56 11.56	$1.74 \\ 1.74 \\ 1.74 \\ 1.74$	$2.22 \\ 3.09 \\ 7.44$	2.90 .77 .77	.30 .30 3.15			
19 20 21.:	333	1]]	1 2 3	$3.67 \\ 3.67 \\ 3.67 \\ 3.67$.20 .20 .20	.60 3,60 10.80	$11.56 \\ 11.5$	$1.74 \\ 1.74 \\ 1.74 \\ 1.74$	$2.40 \\ 2.25 \\ 6.62$	4.09 .94 .77	.30 .30 2.96			
22. 23. 24	3 3 3	2 2 2	1 2 3	3.67 3.67 3.67	$1.22 \\ 1.22 \\ 1.22 \\ 1.22$.60 3.60 10.80	$\frac{11.56}{11.56}$ 11.56 11.56	1.74 1.74 1.74	$2.22 \\ 2.61 \\ 7.64$	2.88 .77 .77	.30 .80 2,96			
25 26 27	3 3 3	3 3 3	1 2 3	3.67 3.67 3.67 3.67	$3.67 \\ 3.67 \\ 3.67 \\ 3.67$.60 3.60 J0.80	$\frac{11.56}{11.56}\\11.56$	$1.74 \\ 1.74 \\ 1.74 \\ 1.74$	3.08 4.38 9.27	1.97 .86 .77	.98 1.37 3.78			

¹Henvy metals were supplied at rates of Fe = 16, Mn = 8, Zn = 0.25, and Cu = 0.075 parts per million. One-tenth p.p.m. (part per million) of boron was supplied from H_3BO_3 . At was supplied as impurities in sand, water, and chemicals used. ² N is expressed as NO₃ nitrogen, although one-fourth of the N was supplied as ammonia.

⁴ Includes SO₄ from sulfates in which heavy metals were supplied.

from the nitrate ion. Under these conditions shifts in pH were much less pronounced and no symptoms of iron deficiency appeared.

EXPERIMENTAL DESIGN AND PLANTING PLAN

The 27 treatments in the experiment were made up from the 3 by 3 by 3 factorial arrangement of the 3 levels of potassium (K-1, K-2, K-3), magnesium (Mg-1, Mg-2, Mg-3), and calcium (Ca-1, Ca-2, Ca-3), as shown in table 4. The experimental unit consisted of 2 crocks, each containing 1 plant. The experimental design used was a randomized block with 4 replications, so arranged that each replication occurred in each

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quarter of the greenhouse from east to west and from north to south. Thus, each treatment was represented by 8 plants, grouped in 4 pairs, 1 pair for each replication.

The frames on which the crocks were arranged were 14 feet long and 6 feet wide and were placed on each side of the center walk of the greenhouse with 2-foot aisles between frames to allow access to the plants from the walk. The crocks were arranged on the frames in three rows of four crocks each. The crocks were spaced 43 inches apart on center in the rows. The crocks in the center row were staggered so as to be 33 inches on center from the crocks in the adjacent outside rows.

GROWTH MEASUREMENTS AND HARVESTING METHODS

The characteristics of growth that may be most important to the perpetuation of the species under natural conditions are often not the most important from the standpoint of the economic use for which the plant is intended when put under cultivation. Since the various criteria of growth may be affected differently by the same environmental changes, it is well, in a study of the kind herein reported, to record as many growth measurements as practicable. By so doing, it is not only possible to detect effects that might otherwise be overlooked, but information may be obtained on the specific functions of the nutrient elements under study.

During the growing season observations were made on the type of growth made by the trees in the different treatments and the time of appearance and rate of development of any symptoms of abnormal nutrition. In addition, the following quantitative measurements were made:

- 1. The height, in centimeters, of each plant was recorded at weekly intervals. Measurement was made from the cotyledonary node to the tip of the terminal bud. As only an occasional plant produced laterals, it was not considered advisable to allow them to develop and complicate growth measurements. Therefore, they were removed as soon as they appeared and a record was kept of the number removed and the dates of removal.
- 2. The diameter of the trunk, in centimeters, at a point approximately 1 cm. below the cotyledonary node was recorded for each plant at the time of harvest.
- 3. The areas, in square centimeters, of the two median leaves on each plant were determined just prior to harvest. Leaf area was determined by multiplying the length of the leaf from point of attachment of the petiole to the leaf tip by the width as measured between the tips of the lobes of the leaf. Actual leaf-area determination showed this method to be very accurate. These leaves composed the samples for chemical analysis.
- 4. During the course of the experiment, all leaves that dropped were collected daily and their dry weights were recorded. This gave a record of rate of leaf fall.
- 5. At harvest the leaves remaining on the plant were removed, their number recorded, and green and dry weights determined. This permitted the determination of total weight of leaves and percentage of total leaf weight that dropped prior to harvest.

- 6. The number of nodes per plant was determined from the total number of leaves produced.
- 7. The average length of internodes was determined by dividing the height of the plant by the number of nodes.
- 8. The plants were removed from the crocks by washing with water under pressure. After removal their root system was freed from sand by further washing. The roots were then spread out on papers and allowed to dry until free of all surface moisture. The succulent feeding roots were separated from the woody storage roots, the storage roots and stems separated at the transition zone, and green weights of feeding roots, storage roots, and stems were recorded.
- 9. All plant parts were dried in a forced draft oven at approximately 80° C., and dry weights were recorded. This permitted calculation of total green and dry weights of each plant.
- 10. Those leaves on which area determinations had been made were dried separately and stored for subsequent nitrogen and mineral analyses.
- 11. Specific-gravity determinations were made on wood samples consisting of the 10- to 15-cm. portion of the stem immediately above the root-stem transitional zone.
- 12. From the total weight of leaves produced and the dry weight of the stems and roots, an estimate of the weight of stems and roots produced per unit weight of leaf was made.

The plants were harvested at random after growth in height had stopped and the terminal buds had formed. The harvesting was done between September 17 and 24, 1945.

ANALYTICAL METHODS

LEAF SAMPLES

The 2 median leaves from each plant taken for leaf area measurements were used as samples for chemical analysis. The 4 leaves from the 2 plants in each treatment plot were combined, but each replication was kept separate and analyzed individually for a total of 12 elements. Ten of these elements were determined by the spectrographic method. Only the leaf blade was included in the sample, the petiole being cut off at the point of attachment to the blade and discarded. The leaf samples were dried in a forced draft oven at approximately 80° C. until dry and then stored in kraft paper bags.

Total nitrogen was determined by the Kjeldahl-Gunning method, to include nitrates and nitrites (6). Zinc was determined essentially as outlined by Cowling and Miller (7).

SPECTROGRAPHIC METHOD

A large Littrow spectrograph with quartz optical parts was used with a slit width of 40μ and length of 1 mm, to analyze and separate 10 of these elements.

The dried leaf samples were ground to 40-mesh in an intermediate Wiley mill (Plant Industry model), dried again at 100° C., and stored in a desiccator. Ten milligram aliquots were weighed on a torsion bal-

ance for determining magnesium, calcium, manganese, aluminum, iron, and copper, while 20 mg, were used for the boron, phosphorus, sodium, and potassium determinations. All determinations were made in triplicate. Each aliquot was transferred quantitatively to machine-drilled craters of graphite electrodes (spectroscopic carbons 5/16 inch in diameter (17)). In analyses for the boron and phosphorus, special high-purity graphite electrodes were used. For all the other determinations, regular spectroscopic carbons (extracted with HCl) were used. The crater depth was 3.5 mm.; the internal diameter, 3.5 mm.; and the wall thickness, 0.3 mm. It was necessary to machine a crater with a flat bottom having little or no depression. The electrodes containing the weighed samples were placed in holes drilled in a transite block and ashed by bringing the temperature up to 500° in a muffle furnace. The electrodes were allowed to cool immediately to room temperature. A few drops of triple-distilled kerosene containing 8- to 10-percent paraffin were added around the rim of each electrode cavity. The samples were then treated cautiously with a few drops of a dilute (1:7) solution of HCl, and evaporated to dryness at 110° in an electric oven.

Standards were prepared for each plate by appropriate dilution of a stock solution containing known quantities of the elements listed below.

Element :			Conc (mwrogram	centration ¹ (g,) per 0.1 ml.)
K.				1,166.0
Ca				773.0
Р				280.0
Mg				198.6
Na				35.4
Fe	.			20.1
Al				19.5
Mn				10.4
Cu				2.4
В	• •	 		2.5

¹Stock solutions were diluted with 1:10 HCl solutions to yield the following fractional concentrations: 0.8, 0.6, 0.4, 0.3, 0.2, 0.1, 0.05, 0.025, 0.015.

One-tenth-milliliter quantities of the correctly diluted standard solutions were transferred by means of a precision pipette to the craters of electrodes, pretreated with the kerosene paraffin mixture, and then evaporated to dryness.

The electrode craters with sample residue (and standard) served as anodes in a direct-current arc; the upper, or cathode, electrode was a tapered 1/8-inch carbon rod. The arc was rotated magnetically by means of an alnico magnet approximately 3 inches away, mounted on a small induction motor (19). A 2-mm, interelectrode distance was maintained during the arcing period by continuous adjustment of the electrodes, using as guides electrode images focused in juxtaposition to fiducial marks on the laboratory wall. The arc image was focused on the collimating lens inside the spectrograph, where a mask eliminated the glowing electrodes. The current was controlled by a rheostat at 24 to 22 amperes. The applied voltage was 140 to 130 volts from a motor generator reserved for the purpose. A ballast resistance of 20 ohms consisted of 1/8- by 1/32-inch Nicrome ribbon wound on a transite board. An arc starter (4) was used. An exposure time of 60 to 70 seconds was sufficient for complete volatilization of each sample. A shorter exposure time (30 to 35 seconds) was chosen (after moving plate studies) for the sodium and potassium determinations. After exposure, the plates (Eastman III-0) were developed for 5 minutes in solution D-19 at 18° C., then fixed, washed, and dried.

Data are based on measurement of the following lines:

Element :	Wave length	Element:	Wave length
Al	3082.2	К	3446.7
B	2496.8	Na	3302.9
	2997.3	Mg	2781.4
Fo	3247.5	Man	2801.1
FC	0020.0	£	2553.3

The percentage of transmission of light through the lines was determined by the use of an Applied Research Laboratories nonrecording densitometer. The measured transmissions of selected lines in the standards permitted the construction of working curves of log concentration vs. log percent transmission. With percent transmissions of known lines for the elements in the test sample, the logarithms of the concentrations of these elements could be read directly from the standard curves. The method used external standards on every plate where standard solutions containing all the elements were burned off in the arc under the controlling influence of a buffer (NaCl + H₂SiO₃, 9:1) added to both samples and standards. The buffer was added by volume (introduced into the electrode quickly from a hole in the end of a plastic rod). The amount of buffer used on top of all the standards and samples ranged from 4.1 to 4.5 mg. Thus, the method was fast and yet the reproducibility of adding the buffer was adequate.

STATISTICAL METHODS

All data on growth responses and leaf composition as affected by individual elements and combination of elements were studied by means of analysis of variance (11). The data for main effects and interactions are presented in the form of graphs. In general, only the data that have statistical significance have been presented in the graphs or have been stated in the text. An effort has been made to weigh the evidence carefully, both from a statistical and from a physiological point of view.

GROWTH RESPONSES IN RELATION TO NUTRIENT SUPPLY

The wide differences in the three levels of calcium, magnesium, and potassium supplied during the 4½ months of the experiment produced highly significant differences in the growth responses and normality of the plants. The major effects on the growth responses were caused by the levels of magnesium and potassium supplied. The effects of the various levels of calcium, though generally of lesser magnitude, were of high statistical significance in certain instances; as, for example, in affecting the heights of the plants. The highest level of calcium supplied was three times that of potassium or magnesium; therefore, comparisons between responses to potassium or magnesium and those of calcium cannot be made on an equal-milliequivalent basis. Where the nutrients supplied were in proper balance, large, excellent plants, normal in all respects, were produced that would compare favorably with those grown in the field in fertile soil under similar conditions of light and temperatures (fig. 1).



FIGURE 1. - Representative plants from each level of potassium and magnesium at the intermediate level of calcium.

DRY WEIGHT OF PLANT

The total dry weight of plants produced was dependent largely and about equally on the levels of potassium and magnesium in the supply, and the responses to these two elements were interrelated. The average over-all effects for the low, medium, and high levels of potassium were 65.5, 123.2, and 130.5 grams, respectively; for magnesium 65.7, 125.5, and 127.9 grams, respectively (table 5; fig. 2).

At the low level of magnesium, the greatest increase in dry weight of plant resulted from the first increment of potassium, but the second increment of potassium produced plants having dry weights intermediate between those at the K-1 and K-2 levels (fig. 2, A).

At the second and third levels of magnesium, both first and second increments of potassium affected increases in dry weight, but the greater increase resulted from the first increment. At all levels of potassium, the first increment of magnesium increased dry weight, but the second increment produced a further increase only at the low level of potassium.

At all levels of potassium and magnesium, the first increment of calcium tended to increase, and the second to decrease plant dry weight. The average weights per plant were 107.2, 111.4, and 100.6 grams for the low, medium, and high levels of calcium, respectively.

DRY WEIGHT OF STEM

The effects of the treatments on the dry weight of stems (table 5) differed in no important respects from those on the total dry weight of plants (fig. 2, A).

DRY WEIGHT OF STORAGE ROOTS

The effects of treatments on dry weight of storage roots (table 5; fig. 2, C and F) were determined largely by the level of magnesium supply, but they also were affected by that of potassium, and the response to these two elements were interrelated. Whereas stem weight was not increased by the second increment of magnesium, storage-root weight was increased by this magnesium increment at all levels of calcium and potassium. The over-all averages per plant were 3.78, 22.5, and 28.4 gm. for the low, medium, and high levels of magnesium, respectively.

The response to potassium was affected by the level of calcium. At the low and medium levels of calcium, the first increment of potassium increased and the second decreased slightly the storage-root weight. At high calcium, both increments of potassium increased storage-root weight (fig. 2, F).

DRY WEICHT OF FEEDING ROOTS

The dry weights of the feeding roots were determined largely by the level of magnesium supply, but they were also affected by the levels of potassium and calcium. Furthermore, the effects of magnesium and potassium were interrelated. In general, these effects were similar to those on the total plant weight (table 5; fig. 2, A and B). The potassium effects differed only slightly from its effects on total plant weight and this only at the low magnesium level, where both increments of potassium tended to reduce feeding-root weight (table 5; fig. 2, B).

TABLE 5.—Effects of various levels of potassium, magnesium, and calcium in the nutrient solution on growth responses of tung trees in sand cultures 1

	Treat	ment			Page 1					1		1			Lagran			B
No.	C.	ompone	nts	Total plant weight	Stem weight	Storage- root weight	Feeding- root weight	Total weight of leaves produced	Stem plus roots weight	Plant height	Nodes per plant	Average length of internodes	Trunk diameter	Leaves dropped	dropped percent total leaf	Average area two median leaves ¹	Leaf effi- ciency ¹ ²	Specific C gravity A of wood
		Mg	L'Ca	<u> </u>			· · · · · · · · · · · · · · · · · · ·	ļ							weight.	 		5 <u>0</u>
$\begin{array}{c} 1 \ldots \\ 2 \ldots \\ 3 \ldots \end{array}$	1 1 1	1 1 1	1 2 3	Gm. 53.7 53.8 47.1	Gm. 6.78 6.22 4.78	Gm. 5.15 4.65 2.95	Gm. 6.32 5.82 3.62	Gm. 35.48 37.15 35.72	$Gm. \\ 18.25 \\ 16.69 \\ 11.35$	Cm. 30.3 28.2 26.8	No. 22.5 23.5 25.2	Cm. 1.347 1.205 1.065	Cm. 0.878 .876 .805	Gm. 26.7 26.1 27.0	75.2870.3175.82	Cm. 259.0 279.2 265.0	$0.515 \\ .448 \\ .318$	0.788 .775 .741
$\begin{array}{c} 4\ldots \\ 5\ldots \\ 6\ldots \end{array}$	1 1 1	$\begin{vmatrix} 2\\2\\2 \end{vmatrix}$	$\begin{vmatrix} 1\\ 2\\ 3 \end{vmatrix}$	$ \begin{array}{r} 65.7 \\ 71.9 \\ 66.1 \end{array} $	$9.52 \\ 10.95 \\ 10.10$	$11.68 \\ 15.75 \\ 11.28$	$12.15 \\ 12.05 \\ 10.65$	$32.30 \\ 33.18 \\ 34.08$	$33.35 \\ 38.75 \\ 32.03$	$32.7 \\ 32.6 \\ 32.8$	$\begin{array}{c} 21.4\\ 21.6\\ 21.9\end{array}$	$1.534 \\ 1.509 \\ 1.503$	$1.001 \\ 1.046 \\ .991$	$\begin{array}{c} 11.0\\ 4.5\\ 4.4\end{array}$	$34.25 \\ 13.44 \\ 12.77$	$238.2 \\ 268.0 \\ 267.8$	$1.032 \\ 1.180 \\ .940$.784 8 .815 .803 .
7 8 9	1 1 1	3 3 3	1 2 3	$74.5 \\ 82.9 \\ 73.7$	$11.70 \\ 13.48 \\ 10.78$	$18.95 \\ 19.35 \\ 16.78$	$12.18 \\ 14.58 \\ 12.78$	$31.68 \\ 35.50 \\ 33.40$	$\begin{array}{r} 42.83 \\ 47.41 \\ 40.34 \end{array}$	$34.3 \\ 35.8 \\ 32.8$	$20.2 \\ 21.8 \\ 21.9$	$1.710 \\ 1.662 \\ 1.498$	$1.062 \\ 1.108 \\ 1.084$	$4.9 \\ 4.2 \\ 3.9$	$15.08 \\ 12.14 \\ 11.81$	$269.0 \\ 283.8 \\ 285.2$	$1.378 \\ 1.332 \\ 1.208$.786 .807 DEP .790 P
10 11 12	2 2 2	1 1 1	1 2 3	$86.2 \\ 91.6 \\ 71.7$	$8.88 \\ 10.75 \\ 6.30$	$5.32 \\ 6.42 \\ 3.05$	$5.25 \\ 5.12 \\ 1.48$	$\begin{array}{c} 66.78 \\ 69.30 \\ 60.85 \end{array}$	$19.45 \\ 22.29 \\ 10.83$	$49.3 \\ 50.8 \\ 38.6$	$29.4 \\ 29.6 \\ 31.6$	$1.678 \\ 1.717 \\ 1.220$	$.978\\1.025\\.866$	$54.4 \\ 55.1 \\ 53.6$	$81.30 \\ 79.50 \\ 88.20$	$345.5 \\ 340.8 \\ 218.5$.298 .320 .172	.683 .692 .642 A
13 14 15	$2 \\ 2 \\ 2$	2 2 2	$\begin{array}{c}1\\2\\3\end{array}$	$139.1 \\ 152.1 \\ 136.5$	$27.00 \\ 28.98 \\ 26.10$	$24.28 \\ 29.85 \\ 26.35$	$26.28 \\ 27.50 \\ 25.10$	$\begin{array}{c} 61.32 \\ 65.80 \\ 58.98 \end{array}$	$77.56 \\ 86.33 \\ 77.55$	$71.8 \\ 69.6 \\ 59.4$	$28.0 \\ 26.5 \\ 25.4$	$2.564 \\ 2.635 \\ 2.343$	${}^{1.311}_{1.396}\\{}^{1.300}$	$2.6 \\ 2.4 \\ 3.6$	$4.37 \\ 3.68 \\ 6.18$	$\begin{array}{c} 414.0 \\ 436.5 \\ 412.8 \end{array}$	${}^{1.268}_{1.320}_{1.320}$.764 GRICU .752 ICU .771 U
16 17 18	2 2 2	3 3 3 3	$egin{array}{c} 1 \\ 2 \\ 3 \\ \end{array}$	$150.7 \\ 145.1 \\ 135.4$	$29.72 \\ 27.72 \\ 25.00$	$33.40 \\ 32.78 \\ 30.40$	$25.75 \\ 27.78 \\ 24.00$	$\begin{array}{c} 61.78 \\ 56.82 \\ 56.00 \end{array}$	$ \begin{array}{r} 88.87 \\ 88.28 \\ 79.40 \end{array} $	$70.6 \\ 67.6 \\ 59.0$	$26.5 \\ 26.4 \\ 24.4$	$2.660 \\ 2.561 \\ 2.426$	$\substack{1.420\\1.388\\1.329}$	$2.5 \\ 2.5 \\ 2.8$	$4.03 \\ 4.40 \\ 4.91$	$ \begin{array}{r} 400.5 \\ 401.8 \\ 414.8 \end{array} $	$1.442 \\ 1.570 \\ 1.412$.743 .736 .777 E
$\begin{array}{c} 19\ldots \\ 20\ldots \end{array}$	3 3	1 1	$\frac{1}{2}$	$\begin{array}{c} 64.2 \\ 67.5 \end{array}$	$\begin{array}{c}4.55\\5.02\end{array}$	2.25 2.50	$1.82 \\ 1.42$	$\begin{array}{c} 55.62\\ 58.58 \end{array}$	$\begin{array}{c} 8.62 \\ 8.94 \end{array}$	$\begin{array}{c} 37.9\\ 35.6 \end{array}$	$\begin{array}{c} 31.6\\ 32.4 \end{array}$	$1.190 \\ 1.096$.811 .821	$49.8 \\ 52.2$	89.81 89.08	209.8 203.2	$.152 \\ 152$.608

[All data given are averages of four two-plant replications]

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21	3		3	55.9	3.70	1.68	.58	49.92	5.96	30.1	32.6	.923	.775	44.3	88.70	180.8	.120	.547
$\begin{array}{c} 22\ldots \\ 23\ldots \\ 24\ldots \end{array}$	3 3 3	$\begin{array}{c} 2\\ 2\\ 2\\ 2\end{array}$	1 2 3	$170.6 \\ 167.6 \\ 160.2$	$ \begin{array}{r} 37.58 \\ 34.02 \\ 30.65 \end{array} $	$25.65 \\ 28.45 \\ 29.62$	$31.22 \\ 30.05 \\ 27.42$	$76.10 \\ 75.10 \\ 72.45$	$\begin{array}{r} 94.45 \\ 92.52 \\ 87.69 \end{array}$	$ \begin{array}{r} 89.7 \\ 80.3 \\ 71.2 \end{array} $	$29.6 \\ 29.5 \\ 27.1$	$3.030 \\ 2.726 \\ 2.622$	$1.378 \\ 1.354 \\ 1.364$	$4.8 \\ 7.1 \\ 7.0$	$6.25 \\ 9.36 \\ 9.83$	$\begin{array}{r} 438.8 \\ 428.5 \\ 440.2 \end{array}$	$1.242 \\ 1.232 \\ 1.208$.791 .784 .787
$\begin{array}{c} 25\ldots \\ 26\ldots \\ 27\ldots \end{array}$	3 3 3	3 3 3	1 2 3	$160.1 \\ 169.9 \\ 159.3$	$\begin{array}{r} 32.10 \\ 34.15 \\ 30.32 \end{array}$	$32.02 \\ 35.08 \\ 36.32$	$28.68 \\ 27.62 \\ 26.42$	$\begin{array}{c} 67.25 \\ 73.00 \\ 66.22 \end{array}$	$92.80 \\ 96.85 \\ 93.06$	$77.8 \\ 75.9 \\ 67.4$	$27.4 \\ 28.8 \\ 26.8 $	$2.811 \\ 2.635 \\ 2.523$	$1.355 \\ 1.425 \\ 1.390$	${3.4} \\ {2.9} \\ {2.9} \\ {2.9}$	$4.94 \\ 3.93 \\ 4.36$	$\begin{array}{r} 413.2 \\ 418.0 \\ 410.5 \end{array}$	$1.382 \\ 1.328 \\ 1.405$.767 .769 .765
L.S.D leve L.S.D leve	. at 5 1 . at 1 1	i-perce -perce	ent ent	11.9 15.8	3 .97 5.29	4.00 5.33	2.90 3.87	6.43 8.57	8,23 10,96	8.3 11.1	1.9 2.5	. 285 . 380	.076 .100	4.7 6.3	5.37 7.15	56.0 74.6	. 159 . 210	.025 .046

^a The figures in any column of measurements that involve ratios cannot be obtained by performing the appropriate calculation with the figures in this table which are involved in that ratio, because these ratios are averages of replications and are not calculated from the averages of the measurements involved. ^a Leaf efficiency calculated as dry weight of stem plus roots divided by dry weight of leaves produced.

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NUTRIENT ELEMENT BALANCE IN TUNG TREES



FIGURE 2.—Interactions of potassium and magnesium on dry weights of (A) plant, (B) feeding roots, (C) storage roots, (D) leaves, (E) stem plus roots; and interaction of potassium and calcium on dry weight of (F) storage roots.

DRY WEIGHT OF LEAVES PRODUCED

The total dry weight of leaves produced (table 5; fig. 2, D) was affected largely by the level of potassium supply and in a manner similar to that of total plant weight (fig. 2, A), excepting that the effect of magnesium was much less pronounced. Increasing the amount of magnesium produced small but significant increases in leaf weight per plant only at the high level of potassium. At the high potassium level the second level of magnesium produced much more dry weight of leaves than did the high level of magnesium. At the second level of potassium increasing the levels of magnesium. At the second level of potassium increasing the levels of magnesium significantly reduced total dry weight of leaves produced, which were 65.6, 62.0, and 58.2 gm. for the low, medium, and high levels of magnesium, respectively. Increasing the amount of calcium tended to produce an increase in dry weight with the first increment, but the second one resulted in a highly significant decrease as compared to the first.

DRY WEIGHT OF STEM PLUS ROOTS

The total dry weight of stem plus roots (table 5; fig. 2, E) was determined largely by the supply of magnesium and potassium, but calcium had highly significant effects. These effects differed from those for total dry weight of plant (fig. 2, A) largely in that at the low level of magnesium there was no significant effect on the dry weight of stem plus roots from the first increment of potassium, whereas the second increment of potassium caused a marked reduction.

PLANT HEIGHT

The level of potassium supply was the major factor that affected plant height (table 5; fig. 3, A and F). The average effects at all levels of calcium and magnesium were 31.8, 59.6, and 62.9 cm, for the low, medium, and high levels of potassium, respectively. The potassium effect was modified by the level of magnesium and to a lesser extent by that of calcium. At all levels of calcium, both increments of potassium increased plant height at the medium and high levels of magnesium. At the low magnesium level, however, only the first increment of potassium increased plant height, the height at the high potassium level being signific untly less than that at the intermediate level. At all levels of magnesium and the intermediate and high levels of potassium, increasing the calcium supply resulted in reduced height of the plants (fig. 3, F).

NUMBER OF NODES PER PLANT

The supply of potassium had the major effect on number of nodes produced (table 5; fig. 3, E_1 , which increased significantly with each increment. On the other hand, increasing the level of magnesium supply reduced significantly the number of nodes produced (fig. 3, E_1 , while the addition of calcium had little and no consistent effect.

LENGTH OF INTERNODES

Increasing either or both potassium and magnesium supply tended to increase internode length (table 5; fig. 3, B); the effect of each being greater, the higher the level of the other. However, at the high level of potassium, the intermediate level of magnesium resulted in longer inter-



FIGURE 3.—Interactions of potassium and magnesium on (A) plant height, (B) average length of internodes, (C) dry weight of leaves dropped, (D) the percentage of total leaf weight dropped. Average effects of potassium and magnesium on (E) number of nodes per plant; and interaction of calcium and potassium on (F) plant height.

nodes than did the high level of magnesium. Furthermore, at the low level of magnesium, the second increment of potassium reduced internode length as compared with the first. Increasing calcium had the effect of reducing internode length at all levels of magnesium and potassium; the average readings were 2.061, 1.972, and 1.791 cm. for Ca-1, Ca-2, and Ca-3 levels, respectively.

DIAMETER OF TRUNK

Trunk diameter (table 5) was affected in a similar way as was total dry weight of plant (fig. 2, A), excepting that at the second and third levels of magnesium, the second increment of potassium did not effect so large an increase in trunk diameter as it did in plant weight. Furthermore, the average effects at all levels of potassium and magnesium was for the first increment of calcium to increase and the second increment to reduce the diameter of the trunks. The averages for the low, medium, and high levels of calcium were 1.133, 1.160, and 1.100 cm., respectively, a difference of 0.025 being required for significance at the 5-percent level.

LEAVES DROPPED

Leaf drop, considered either on the basis of total dry weight dropped or as the percentage of the total leaf weight produced which dropped, was caused mainly by magnesium deficiency (table 5, fig. 3, C and D). At all levels of calcium and the low level of magnesium, the percentage of leaves that dropped increased markedly with the first increment of potassium and slightly with the second. Minor variations occurred at the second and third levels of magnesium, which, when considered on a percentage basis, were considerably higher in the K-1 than in the K-2 and K-3 treatments. Though calcium did not significantly affect either actual weight or percentage of total leaf weight dropped, at the low level of potassium and magnesium leaf fall commenced in the Ca-3 treatment 37 days before and in the Ca-2 treatment 21 days before it did in the Ca-1 treatment. At the low level of magnesium and at the two higher levels of potassium, there was no significant difference in time of onset of leaf fall caused by level of calcium supply.

AVERAGE AREA OF TWO MEDIAN LEAVES

Leaf size was controlled mainly by the supply of potassium and magnesium, while the level of calcium had no significant effect (table 5; fig. 4, A). The largest leaves were produced with the second and third levels of magnesium combined with the second and third levels of potassium. At the first level of potassium there was no consistent effect of magnesium. At the low level of magnesium the first increment of potassium increased leaf size slightly, but the second increment decreased it to a marked degree.

LEAF EFFICIENCY

The major factor affecting leaf efficiency (dry weight of stem plus roots per gram of leaf dry weight) was the magnesium supply (table 5; fig. 4, B), but there were important interactions with potassium. The greatest efficiency was obtained at the high level of magnesium combined with either the second or third level of potassium. Efficiency was



FIGURE 4.—Interactions of polassium and magnesium on (A) the average area of two median leaves, (B) the dry weight of stems plus roots per gram of leaf, (C) the specific gravity of wood.

significantly less when the second and third levels of potassium were combined with the second level of magnesium. At low magnesium, increasing potassium decreased leaf efficiency, the lowest efficiency being at low magnesium, high potassium levels. Leaf efficiency was significantly affected by the level of calcium supply, being lower at the Ca-3 level than at the Ca-1 or Ca-2 levels.

SPECIFIC GRAVITY OF WOOD

Specific gravity of the wood was affected most by the magnesium supply, although it was significantly affected by the level of potassium, and there were important interactions between potassium and magnesium (table 5; fig. 4, C). The first increment of magnesium produced highly significant increases in specific gravity of the wood, but the second increment resulted in nonsignificant decreases. The over-all effect of potassium was to reduce specific gravity, the averages being 0.788, 0.729, and 0.710, respectively, for the K-1, K-2, and K-3 levels. At all levels of calcium, the lowest specific gravity, 0.575, resulted at low mag-

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nesium, high potassium levels, and the highest, 0.801, at the low potassium and intermediate magnesium levels. Calcium significantly affected specific gravity only at the low level of magnesium, where it brought about a highly significant reduction.

CHEMICAL COMPOSITION OF LEAVES IN RELATION TO NUTRIENT SUPPLY

The composition of the leaves as regards each of the 12 elements determined were significantly affected by the differences in calcium, magnesium, and potassium supplied in the solutions.

NITROCEN

Although the nutritive solutions supplied contained 11.56 milliequivalents per liter (m.e./l.) of nitrogen, its content in the leaves ranged from 970 to 713 m.e. per 100 gm. dry matter (table 6).

The nitrogen in the leaves was inversely proportional to the level of magnesium supply, the level of potassium supply, and the level of calcium supply (fig. 5). The effect of calcium was most pronounced at the low level of magnesium, and the effect of magnesium was greatest at the low level of calcium, whereas the effect of potassium was greatest at the low level of either magnesium or calcium or of both. The departures from the expected levels of nitrogen were of a minor importance.



FIGURE 5.—The over-all effect of potassium, magnesium, and calcium in the nutrient solution on the nitrogen content (milliequivalents per 100 gm, of dry matter) of the leaves.

Treatment				Mulliequivalents per 100 grams of dry weight of -																
																			Tatal	
No.	Con	nponei	its	N+++	P++++	- K+	Ca++	Mg++	Na+	B+++	Cu++	Mn⁺≁	Zn++	Fe+++	Al+++	Cn + Mg + K	K + Mg	Ca + Mg	Ca + K	heavy metals + B 1
••••••••••••••••••••••••••••••••••••••	ĸ	Mg	Ca											- 1		-	-			
1 2 3	1 1 1	1 1 1	1 2 3	970.0 904.0 906.0	$125.4\\108.5\\102.8$	$30.9 \\ 28.5 \\ 30.2$	$47.4 \\ 75.6 \\ 116.3$	10.4 7.1 6.4	$\begin{array}{r} 0.40 \\ .46 \\ .51 \end{array}$	$3.56 \\ 3.21 \\ 2.99$	$\begin{array}{r} 0.0247 \\ .0256 \\ .0244 \end{array}$	$3.86 \\ 3.42 \\ 3.06$	$0.70 \\ .47 \\ .52$	$0.60 \\ .73 \\ .62$	$\substack{1.34\\1.59\\1.38}$	$88.7 \\ 111.2 \\ 152.9$	$\begin{array}{c} 41.3 \\ 35.6 \\ 36.8 \end{array}$	$57.8 \\ 82.7 \\ 122.7$	$78.3 \\ 104.1 \\ 146.5$	$10.092 \\ 9.431 \\ 8.572$
4. 5. 6.	1 1 1	2 2 2	1 2 3	$ 846.0 \\ 801.0 \\ 803.0 $	$105.3 \\ 114.4 \\ 133.8$	$18.9 \\ 14.0 \\ 16.0$	$38.2 \\ 85.3 \\ 132.4$	$32.0 \\ 40.4 \\ 43.0$	$.83 \\ .46 \\ .39$	$3.70 \\ 2.76 \\ 2.61$.0282 .0260 .0275	$4.03 \\ 4.27 \\ 3.41$	$.53 \\ .39 \\ .36$	$\begin{array}{r} .81\\ .94\\ 1.08\end{array}$	$2.14 \\ 2.79 \\ 2.53$	$89.1 \\ 139.7 \\ 191.4$	50.9 54.4 59.0	$70.2 \\ 125.7 \\ 175.4$	$57.1 \\ 99.3 \\ 148.4$	11.234 11.159 10.013
7. 8. 9.	1 1 1	3 3 3	1 2 3	$\begin{array}{c} 822.0 \\ 795.0 \\ 747.0 \end{array}$		$13.7 \\ 12.5 \\ 14.5 \\ $	$25.0 \\ 71.9 \\ 108.2$	$44.4 \\ 57.1 \\ 62.2$.37 .34 .33	${3.02 \atop {3.13} \atop {3.23}}$	$.0258 \\ .0263 \\ .0241$	$3.72 \\ 3.31 \\ 2.88$.42 .33 .21	.77 .84 .90	$2.07 \\ 2.79 \\ 2.50$	$83.1 \\ 141.5 \\ 184.9$	$58.1 \\ 69.6 \\ 76.7$	$69.4 \\ 129.0 \\ 170.4$	$38.7 \\ 84.4 \\ 122.7$	$10.018 \\ 10.416 \\ 9.752$
10 11 12	2 2 2	1 1 1	$1 \\ 2 \\ 3$	$ \begin{array}{r} 921.0 \\ 840.0 \\ 735.0 \end{array} $	$47.2 \\ 56.1 \\ 48.8$	$\begin{array}{c} 62.9 \\ 59.0 \\ 59.5 \end{array}$	$27.8 \\ 59.0 \\ 72.1$	$\begin{array}{c} 5.2\\ 4.4\\ 3.9\end{array}$	$.96 \\ .84 \\ .79$	$\substack{1.81\\1.60\\1.67}$	$.0201 \\ .0179 \\ .0132$	$3.42 \\ 2.97 \\ 1.83$. 38 . 35 . 18	$.51 \\ .60 \\ .46$	$\substack{1.24\\1.90\\1.42}$	$\begin{array}{r} 95.9 \\ 122.4 \\ 135.5 \end{array}$	$68.1 \\ 63.4 \\ 63.4$	$33.0 \\ 63.4 \\ 76.0$	90.7 118.0 131.6	$7.378 \\ 7.425 \\ 5.571$
13, 14 15	2 2 2	2 2 2	1 2 3	777.0 720.0 717.0	$46.7 \\ 40.3 \\ 52.4$	$38.0 \\ 30.1 \\ 37.7$	$33.9 \\ 82.1 \\ 135.0$	$21.1 \\ 22.1 \\ 17.0 \\$.95 .77 .58	$1.44 \\ 1.30 \\ 1.50$	$.0169 \\ .0183 \\ .0195$	$3.45 \\ 3.65 \\ 2.63$.27 .25 .24	.61 .66 .84	$1.79 \\ 2.30 \\ 2.84$	$\begin{array}{r} 93.0 \\ 134.3 \\ 189.7 \end{array}$	$59.1 \\ 52.2 \\ 54.7$	$55.0 \\ 104.2 \\ 152.0$	$71.9\\112.2\\152.0$	$7.570 \\ 8.174 \\ 8.124$
16. 17. 18	2 2 2	3 3 3	1 2 3	$724.0 \\ 713.0 \\ 726.0$	$\begin{array}{r} 44.3 \\ 49.6 \\ 47.5 \end{array}$	$\begin{array}{c} 29.1\\ 26.0\\ 31.7\end{array}$	$22.7 \\ 72.0 \\ 93.6$	$34.0 \\ 36.6 \\ 30.1$	$.64 \\ .55 \\ .59$	$\substack{1.43\\1.38\\1.51}$.0179 .0168 .0175	$3.59 \\ 3.20 \\ 2.44$	$.32 \\ .24 \\ .23$	$.57 \\ .56 \\ .57$	$1.63 \\ 2.01 \\ 1.95$	$85.8 \\ 134.6 \\ 155.4$	$\begin{array}{c} 63.1 \\ 62.6 \\ 61.8 \end{array}$	56.7 108.6 123.7	$51.8 \\ 98.0 \\ 125.3$	7.543 7.394 6.707
19. 20. 21.	3 3 3	1 1 1	1 2 3	$\begin{array}{c} 852.0 \\ 822.0 \\ 750.0 \end{array}$	$44.8 \\ 62.5 \\ 54.8$	$85.7 \\ 76.3 \\ 77.9$	$19.3 \\ 43.1 \\ 58.6$	$\begin{array}{c} 5.1\\ 4.5\\ 4.0\end{array}$.71 .73 .86	$1.38 \\ 1.01 \\ 1.14$	$.0152 \\ .0144 \\ .0126$	$2.51 \\ 2.18 \\ 1.58$.37 .26 .18	$.47 \\ .43 \\ .46$	$1.26 \\ 1.22 \\ 1.25$	$110.1 \\ 123.9 \\ 140.5$	90.8 80.8 81.9	$24.4 \\ 47.6 \\ 62.6$	$105.0 \\ 119.4 \\ 136.5$	$\begin{array}{c} 6.349 \\ 5.402 \\ 4.630 \end{array}$

TABLE 6.—Effects of various levels of potassium, magnesium, and calcium in the nutrient solution on the mineral S composition of leaves from tung trees grown in sand cultures

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$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	775.0 758.0 713.0	$43,2 \\ 44.3 \\ 41.9$	$\begin{array}{c} 69.7 \\ 60.9 \\ 63.6 \end{array}$	$24.6 \\ 61.6 \\ 99.1$	$14.0 \\ 16.6 \\ 12.2$.99 .88 .92	$1.08 \\ 1.08 \\ 1.28$	$.0155 \\ .0156 \\ .0154$	${3.47 \atop 2.76 \atop 2.64}$	$.36 \\ .24 \\ .25$.57 .64 .68	$1.46 \\ 2.25 \\ 2.10$	$108.3 \\ 139.1 \\ 174.9$	$83.7 \\ 77.5 \\ 75.8$	$38.6 \\ 78.2 \\ 111.3$	$\begin{array}{r} 94.3 \\ 122.5 \\ 162.7 \end{array}$	$\begin{array}{c} 7.320 \\ 6.969 \\ 6.956 \end{array}$
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	741.0 713.0 724.0	$37.1 \\ 40.0 \\ 40.3$	$\begin{array}{c} 60.0 \\ 47.5 \\ 43.1 \end{array}$	$20.7 \\ 54.5 \\ 83.4$	$26.2 \\ 24.9 \\ 27.0$.88 .80 .77	$1.16 \\ 1.19 \\ 1.35$.0140 .0136 .0148	$2.78 \\ 2.71 \\ 2.40$	$.26 \\ .25 \\ .19$.57 .56 .61	$1.56 \\ 1.86 \\ 2.07$	$106.9 \\ 126.9 \\ 153.5$	$ \begin{array}{r} 86.2 \\ 72.4 \\ 70.1 \end{array} $	$46.9 \\ 79.4 \\ 110.4$	$80.7 \\ 102.0 \\ 126.5$	$\begin{array}{c} 6.339 \\ 6.579 \\ 6.652 \end{array}$
L.S.D. at 5-percent level L.S.D. at 1-percent level	$\begin{array}{c} 51.0\\ 66.0\end{array}$	$\begin{array}{c}15.5\\20.5\end{array}$	$\substack{5.8\\6.7}$	12.0 15.5	$3.4 \\ 4.5$.27 .36	.35 .47	.0028 .0038	.41 .55	.08 .11	.15 .19	.75 1.00	13.7 18.1	$\begin{array}{r} 6.7 \\ 8.9 \end{array}$	$\begin{array}{c} 12.8\\ 16.9\end{array}$	$\begin{array}{r} 12.5\\16.6\end{array}$	1.141 1.510

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¹These totals do not equal the totals of the heavy metals plus boron as listed in this table, since the figures for individual ions are the averages of the total of 4 replications, whereas the figures for the total of the heavy metals plus boron are the averages of the totals of the 4 replications each of which is itself the total of the 6 individual ions as determined in that replication.

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FIGURE 6.—Interactions of different levels of magnesium (A to C), potassium (D to F), and calcium (C to I) in the nutrient solution with indicated levels of potassium, calcium, and magnesium, respectively, on the phosphorus content of leaves.



FIGURE 7.—The over-all effects of potassium, magnesium, and calcium in the nutrient solution on the potassium content (milliequivalents per 100 gm. of dry matter) of the leaves.

PHOSPHORUS

Phosphorus was supplied in the nutrient solutions at the constant level of 1.74 m.e. per liter of PO_4 , but its content in the leaves in milliequivalents per 100 gm. of dry matter ranged from 133.8 to 37.1 (table 6; fig. 6). It was reduced to a very marked extent by the first increment of potassium, but the second increment produced little or no further change in phosphorus content (fig. 6, D to F). In plants receiving the low level of potassium and also of calcium, there was a moderate reduction in phosphorus, owing to both the first and second increments of magnesium (fig. 6, A).

The interaction of magnesium with calcium on phosphorus content differed with level of potassium (fig. 6, A to C). At low potassium levels, both increments of magnesium tended to reduce phosphorus at the Ca-1 level, but had little effect at Ca-2. At the Ca-3 level the significant effects were an increase in phosphorus caused by the first increment of magnesium and a decrease caused by the second increment of magnesium. At intermediate potassium there was no significant difference in the effect of magnesium on phosphorus at different levels of calcium. At high potassium the only significant effect was a decrease in leaf phosphorus effected by the first increment of magnesium combined with the second or third level of calcium.

The interaction of potassium with calcium differed with levels of magnesium (fig. 6, G to I). At the low magnesium level both the second and third levels of calcium decreased phosphorus in the K-1 treatment; at the K-2 level there was no significant effect of calcium, but at the 1

K-3 level an increase resulted from the first increment of calcium followed by a decrease with the second increment. At the second magnesium level in the K-1 treatments there was a consistent upward trend in leaf phosphorus with increasing calcium, whereas in the K-2 treatments the first increment of calcium had no effect but the second increment increased the leaf phosphorus content. In the K-3 treatments, increasing calcium had no effect. At the high level of magnesium, leaf phosphorus in K-1 treatments was highest at the second level of calcium, and calcium was without effect in the K-2 and K-3 treatments.

POTASSIUM

Leaf potassium ranged from 85.7 to 12.5 m.e. per 100 gm. dry weight and was affected primarily by the level of supply, but there were highly important interactions with magnesium and calcium (table 6). It increased with potassium in solution, the averages being 19.9, 41.6, and 65.0 m.e. per 100 gm., respectively, for the K-1, K-2, and K-3 treatments (figs. 7 and 8).

Increasing magnesium in the substrate reduced leaf potassium, the averages being 56.8, 38.8, and 30.9 m.c. per 100 gm. for the low, intermediate, and high levels of magnesium, respectively (figs. 7 and 9). The effect of calcium was slight although significant, the over-all effects for the leaf potassium were lower at the intermediate level than at low and high levels of calcium (fig. 7) and were 45.4, 39.5, and 41.5 m.e. per 100 gm. for the low, intermediate, and high levels, respectively.

CALCIUM

Calcium in the leaves (table 6) ranged from 135.0 to 19.3 m.e. per 100 gm. dry matter. The major factor affecting leaf calcium was the level of calcium in solution (fig. 10), the averages being 28.8, 67.2, and 99.9, respectively, for the low, intermediate, and high levels of calcium. Potassium reduced leaf calcium (fig. 8), the extent of the reduction increasing with increasing level of potassium supply. At all levels of potassium and calcium the highest leaf calcium tended to occur at the intermediate level of magnesium (fig. 9), this magnesium effect tending to increase with the level of calcium supply. The effect of magnesium was modified somewhat by level of potassium (fig. 10), the greatest relative difference in leaf calcium resulting from levels of magnesium being in the K-2 treatments.

MAGNESIUM

Magnesium in leaves, expressed as milliequivalents per 100 gm. of dry tissue, ranged from 62.2 to 3.9 (table 6). The major effect was that of the level of magnesium, the averages being 5.7, 24.2, and 38.1, respectively, for the Mg-1, Mg-2, and Mg-3 treatments. Increasing the potassium level exerted a strong depressing effect on magnesium (figs. 7 and 10), the average readings being 33.7, 19.4, and 14.9 at the K-1, K-2, and K-3 treatments, respectively. At the low level of potassium, the magnesium content of the leaves was directly proportional to the level of the calcium in the solution (fig. 10, A to C). At the second level of potassium (fig. 10, D to F), where the average magnesium contents were

NUTRIENT ELEMENT BALANCE IN TUNG TREES

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FIGURE 8.—A to I, Effects of different levels of potassium in the nutrient solution on the accumulation in the leaves of potassium, magnesium, calcium, calcium plus magnesium, and calcium plus magnesium plus potassium.

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FIGURE 9.—A to I, Effects of the different levels of magnesium in the nutrient solution on the accumulation in the leaves of magnesium, potassium, calcium, calcium plus potassium, and calcium plus magnesium plus potassium.

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FIGURE 10.—A to I, Effects of different levels of calcium in the nutrient solution on the accumulation in the leaves of calcium, polassium, magnesium, polassium plus magnesium, and calcium plus magnesium plus polassium.

lower than at the low level of potassium, the first increment of calcium was without effect but the second increment caused a decrease in leaf magnesium. At the low level of magnesium, the trend was for increasing calcium to decrease the magnesium content of the leaves (fig. 10, A, D, and G); at the second level of magnesium, the magnesium content was highest at the intermediate level of calcium (fig. 10, B, E, and H); at the third level of magnesium, the first increment of calcium tended to increase leaf magnesium but the second increment produced no further increase (fig. 10, C, F, and I).

The interaction of potassium with calcium on magnesium accumulation differed with different levels of magnesium. At the high level of magnesium, the depressing effect of potassium increased with increasing calcium (fig. 8, G to I). This tendency was less pronounced at the second level of magnesium (fig. 8, D to F) and practically disappeared at the low level (fig. 8, A to C).

Sodium

Sodium was one of the elements in the nutrient supply that was permitted to vary within limits (p. 6) of 0.77 to 7.38 m.e. per liter (table 4). The concentration of sodium in the leaves was controlled largely by the potassium supply, regardless of the concentration of the sodium in the nutritive solution, and ranged from 0.33 to 0.99 m.e. per 100 gm. (table 6). The average concentrations of sodium in the leaves for the K-1, K-2, and K-3 levels were 0.45, 0.74, and 0.84 m.e. per 100 gm., respectively. The relation between the concentration of potassium in the leaves and that of potassium, magnesium, and calcium in the solution was similar to that of sodium, excepting in the case of magnesium (fig. 7). The first increment of magnesium tended to increase the absorption of sodium and the second to decrease it, the main effects were 0.70, 0.75, and 0.59 m.e. per 100 gm. for the Mg-1, Mg-2, and Mg-3 levels, respectively. On the other hand, the first increment of calcium caused a decrease and the second increment produced no further change in the accumulation of sodium in the leaves.

BORON

Boron in the leaves in milliequivalents per 100 gm, ranged from 3.70 to 1.01 (table 6). The major factor affecting boron in the leaves was level of potassium (fig. 11), the averages being 3.13, 1.52, and 1.19, respectively, for K-1, K-2, and K-3 treatments. At low potassium the first increment of calcium decreased leaf boron, but the second increment effected no further decrease. Magnesium had a tendency to depress boron content of the leaves, which was most pronounced in the Ca-1 treatments.

At the low level of potassium the interaction of magnesium with potassium on boron content of the leaves varied according to the level of calcium in solution. In the Ca-1 treatment leaf boron was significantly lower at the third level of magnesium than at the second. In the Ca-2 and Ca-3 treatments leaf boron did not differ significantly at the first and third levels of magnesium, but was low at the second level of magnesium. The first increment of calcium effected an exceptionally large drop in leaf boron in the Mg-2, K-1 creatment.



FIGURE 11.---A to J. Effects of different levels of potassium in the nutrient solution on the accumulation in the leaves of manganese, zinc, copper, iron, aluminum, boron, and the total of these 6 elements.

COPPER

Leaf copper ranged from 0.0282 to 0.0126 m.e. per 100 gm. (table 6). It was strikingly reduced by the level of potassium supply (fig. 11), the averages being 0.0258, 0.0176, and 0.0146, respectively, for the K-1, K-2, and K-3 treatments. Calcium tended to reduce copper in the leaves only at the low level of magnesium.

Leaf copper in the Ca=3 treatments was significantly higher at the intermediate level of magnesium than at the low and high magnesium levels. At the third level of magnesium, leaf copper was intermediate between that at the first and the second magnesium levels.

MANGANESE

Leaf manganese ranged from 4.27 to 1.58 m.e. per 100 gm. dry matter (table 6). The principal factor affecting leaf manganese was the potassium level in the solution (fig. 11), the averages being 3.55, 3.02, and 2.56, respectively, for the K–1, K–2, and K–3 treatments. The effect of potassium was most pronounced at the low level of magnesium and the least pronounced at the high level. Calcium very significantly reduced leaf manganese, the over-all averages were 3.42, 3.16, and 2.54 m.e. per 100 gm. dry matter, respectively, for the Ca–1, Ca–2, and Ca–3 treatments. Leaf manganese was the highest at the second level of magnesium, the averages being 2.76, 3.37, and 3.00 m.e. per 100 gm. dry matter, respectively, for the Mg–1, Mg–2, and Mg–3 treatments. In the Ca–1, K–2 treatments, however, magnesium level did not significantly affect leaf manganese.

ZINC

Leaf zine ranged from 0.70 to 0.18 m.e. per 100 gm, dry tissue (table 6). The first increment of potassium greatly reduced zine in the leaves (fig. 11). No further reduction was effected by the second increment. The averages were 0.44, 0.27, and 0.26 m.e. per 100 gm, dry tissue, respectively, for the K-1, K-2, and K-3 treatments. The effect of potassium was practically nullified by the combination of high calcium and magnesium (fig. 11, I). Calcium reduced leaf zine at all levels of potassium, and magnesium tended to have a similar effect at all levels of potassium and calcium.

IRON

Iron in the leaves ranged from 1.08 to 0.43 m.e. per 100 gm, dry tissue (table 6). Potassium reduced iron in the leaves at all levels of calcium and magnesium (fig. 11), the averages being 0.81, 0.60, and 0.55, respectively, for the K-1, K-2, and K-3 treatments. Magnesium at the intermediate level increased leaf iron, but at the high level it caused a reduction in iron. There was a general tendency for calcium to increase leaf iron, but differences attained statistical significance only in the Mg-2 treatments.

Aluminum

Aluminum in the leaves ranged from 2.84 to 1.22 m.c. per 100 gm. drv tissue (table 6). It was significantly affected by calcium, magnesium, and potassium. The first increment of magnesium increased aluminum from 1.40 to 2.24, but the second increment had no further effect. Calcium exerted a similar but somewhat less pronounced effect. The overall effect of potassium was to decrease aluminum in the leaves (fig. 11). The averages were 2.13, 1.90, and 1.67 m.e. per 100 gm. dry tissue, respectively, for the K-1, K-2, and K-3 treatments.

CALCIUM PLUS MAGNESIUM PLUS POTASSIUM

The total calcium plus magnesium plus potassium in the leaves (table 6) was controlled largely by the level of calcium supply, but it was also significantly affected by the magnesium supply, the range being 191.4 to 83.1 m.e. per 100 gm, dry leaf tissue. The main factor, calcium in solution, had an over-all effect of 96.0, 130.6, and 164.0 m.e. per 100 gm, for the Ca-1, Ca-2, and Ca-3 levels, respectively. The over-all effects of magnesium at all levels of potassium and calcium were 120.6, 139.9, and 130.3 m.e. per 100 gm., respectively, for the Mg-1, Mg-2, and Mg-3 treatments.

At low levels of calcium there was an upward trend in total major bases with increasing potassium (fig. 8, A, D, and G), but at the second level of calcium (fig. 8, B, E, and H) potassium had no effect and the trend in the ('a-3 treatments (fig. 8, C, F, and I) was the reverse of that in the ('a-1 treatments.

Total accumulation of all the major bases was highest at the second level of magnesium (fig. 9); at the third level it was intermediate between the first and second. This relationship was most pronounced in the Ca-3 treatments (fig. 9, G to I) and disappeared in the Ca-1 treatments (fig. 9, A to C).

POTASSIUM PLUS MAGNESIUM

The total concentration of potassium plus magnesium in the leaves ranged from 35.6 to 90.8 m.e. per 100 gm. (table 6). It was controlled largely by the potassium supply. The averages were 53.6, 60.9, and 79.9 m.e. per 100 gm, for the K-7, K-2, and K-3 levels, respectively. Magnesium supply also had a highly significant effect in increasing the total concentration of potassium plus magnesium present. The general over-all effect of calcium was for the first increment to reduce potassium plus magnesium (fig. 10). This effect was most pronounced in the K-3 treatments (fig. 10, G to I) and disappeared in the K-1 treatments, where the trend was upward with increasing levels of calcium with the second and third levels of magnesium (fig. 10, A, B, and C).

CALCIUM PLUS MAGNESIUM

The total calcium plus magnesium in the leaves ranged from 24.4 to 175.4 m.e. per 100 gm, and was controlled by the supply of calcium and magnesium but was greatly affected by the potassium supply (table 6). The over-all effect of calcium was to increase the calcium plus magnesium in the leaves, which was 50.2, 91.0, and 122.6 m.e. per 100 gm, for the Ca-1, Ca-2, and Ca-3 levels, respectively. The average effect of the first increment increase in magnesium supply was to increase greatly calcium plus magnesium in the leaves, but the second increment of magnesium produced no further change. Potassium in solution strikingly reduced the total calcium plus magnesium in the leaves (table 6; fig. 8), the over-all effects being 111.5, 85.8, and 66.6 m.e. per 100 gm., respectively, for the K-1, K-2, and K-3 levels,

CALCIUM PLUS POTASSIUM

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At the low level of calcium the first and second increments of magnesium reduced the accumulation of calcium plus potassium (fig. 9, A to C). This effect from the first increment of magnesium practically disappeared at the second level of calcium (fig. 9, D to F) and was reversed at the third level (fig. 9, G to I). The second increment of magnesium reduced calcium plus potassium at all levels of calcium.

TOTAL HEAVY METALS PLUS BORON

Total heavy metals (Cu, Mu, Zu, Fe, Al) plus boron in the leaves in milliequivalents per 100 gm, ranged from 11.23 to 4.63 m.e. per 100 gm, dry matter (table 6). The major factor affecting the accumulation of these ions in the leaves was the level of potassium supply (fig. 11), the readings being 10.08, 7.32, and 6.35, respectively, for the K-1, K-2, and K-3 treatments. At the low level of magnesium, the second increment of potassium had a greater depressing effect on the heavy metals plus boron than at the two higher levels of magnesium supply.

Magnesium supply also affected the leaf content of total heavy metals plus boron, the highest content of these ions occurred at the medium level of magnesium supply, while at the high level of magnesium it was intermediate between that in the Mg-1 and Mg-2 treatments.

Calcium had an over-all tendency to reduce the total heavy metal plus boron content in the leaves, the second increment of calcium being the more effective.

INTERPRETATION AND DISCUSSION OF RESULTS

COMPOSITION IN RELATION TO GROWTH AND LEAF SYMPTOMS

The data presented in this bulletin constitute only a small part of the evidence accumulated by the authors to support the concept of the nutrient-element balance that should be maintained in the culture of tung. Data obtained by other investigators give additional support. At the same time, the apparent disagreement between much of the evidence reported and this bulletin tends to emphasize the complexity of the interactions that occur between the essential nutrient elements both in respect to their absorption and accumulation and their effects on growth and yield.

A number of factors are responsible for the lack of agreement between the results of the various investigators. Principal among these is the lack of consistency in the part of the plant used for analysis. It is obviously impossible to compare results of whole-plant analyses with those of leaves or petioles. It is true that the nature of the plant under study and the objective of the investigation influence the selection of the plant part used for analysis. This, however, does not alter the fact that comparisons between analyses of different plant parts are invalid. The variability in mineral content of different plant parts and of leaves from different locations on the shoot has been demonstrated with tung by Myers and Brunstetter (18), who showed that there are large gradients in the mineral content of leaves from different locations on the shoot, and by Drosdoff and Nearpass (8), who showed wide differences to exist between the content of nutrient elements in bottom, middle, and top portions of the petiole as well as differences between all these petiole analyses and those of the leaf blade.

Differences of a similar nature have been shown for other plants. The mineral analyses reported in this bulletin are from leaves collected from the midportion of the growing shoot, and the data presented are not to be construed as indicating absorption phenomena except as such phenomena may be reflected in leaf composition.

Another factor responsible for much apparent disagreement between results of different workers is the range of nutrient levels employed. One outstanding feature of results reported herein is the differential response to the same increments of one element when supplied at different levels of one or more of the other elements. The effects of varying levels of calcium supply on the accumulation of magnesium in the leaves illustrate this point well (fig. 10). When magnesium supply was low, increasing calcium decreased magnesium in the leaves at all levels of potassium supply. With potassium supply low and magnesium supply intermediate or high, magnesium in the leaves increased with increasing calcium. At the second level of potassium and the intermediate and high levels of magnesium, the first increment of calcium did not affect leaf magnesium while the second increment brought about a reduction. At the third level of potassium and the intermediate level of magnesium, the calcium effect was the same as in the intermediate potassium plus intermediate magnesium treatments, but at the high levels of potassium and magnesium combined, calcium supply did not affect accumulation of magnesium in the leaves.

Interpretation of complex interactions such as those just mentioned cannot be made on the basis of cation competition alone. It is obvious that other factors are involved. Identification of these factors will require more knowledge of the function of each cation in metabolism, which can only be obtained by detailed studies of the biochemical changes accompanying these cation interactions.

An illustration of how biochemical studies might contribute to the interpretation of such data may be drawn from the data on the effect of magnesium supply on calcium accumulation (fig. 9) coupled with information obtained from another experiment on the effects of form of nitrogen and amount of base supply on the organic acids of tung leaves (12).

The first increment of magnesium produced an average increase in leaf magnesium of 18.6 m.e. per 100 gm. While this increase in magnesium was accompanied by a reduction of 18.0 m.e. of potassium, calcium increased by 19.2 m.e., or a net increase of 19.8 m.e. in the total potassium, calcium, and magnesium. This increase was also accompanied by a slight increase in total heavy metals plus boron (table 7). Obviously, an equivalent increase must have taken place in anion accumulation. In the absence of analyses for all the mineral anions there is the possibility that they may have contributed to this anion increase.

The most plausible explanation for this cation increase as a result of the first increment of magnesium, however, would seem to lie in the organic acid metabolism. Plants receiving the low level of magnesium made very little growth (table 5) because of severe magnesium deficiency. The first increment of magnesium more than quadrupled leaf efficiency, whereas the second increment produced only a slight further

increase (fig. 4, B). If oxalic acid is an end product of carbohydrate oxidation, as has been suggested (12), it is very probable that at the low level of photosynthetic activity resulting from the extreme magnesium deficiency at the low magnesium level, very little oxalic acid was produced. Under such conditions calcium accumulation would be limited. With the greatly increased leaf efficiency resulting from the first increment of magnesium, calcium accumulation would be expected to increase because of the inactivation of the calcium as oxalate. The second increment of magnesium that resulted in a decrease in both potassium and calcium effected such a slight increase in photosynthetic activity, however, that the increased magnesium accumulation was able to exert a competitive effect on the ionizable calcium that was not removed from the system as oxalate.

TATLE 7.—Effects of supply at 3 levels each of polassium, magnesium, at 1 calcium in the nutrient solution on the accumulation in the leaves if aluminum, boron, copper, iron, manganese, and zinc

Levels of	Milliequivalents per 100 grams of-												
magnesium, and calcium	At	в	('u	Fe	Mn	Zn	Total						
K-i. K-2. K-3 Mg-1. Mg 2 Mg 3 Ca 1 Ca 2 Ca 3	$2.13 \\ 1.90 \\ 1.68 \\ 1.40 \\ 2.25 \\ 2.05 \\ 1.61 \\ 2.08 \\ 2.01 \\ $	$\begin{array}{c} 3.13 \\ 1.51 \\ 1.18 \\ 2.04 \\ 1.86 \\ 1.93 \\ 2.06 \\ 1.85 \\ 1.92 \end{array}$	0.0258 .0176 .0146 .0187 .0203 .0190 .0198 .0194 .0187	0.81 .60 .55 .54 .76 .66 .61 .66 .69	8.55 3.02 2.56 2.76 3.37 3.00 3.42 3.16 2.54	$\begin{array}{c} 0.44 \\ .27 \\ .26 \\ .38 \\ .32 \\ .27 \\ .40 \\ .31 \\ .26 \end{array}$	10.08 7.32 6.35 7.20 8.61 7.93 8.20 8.10 7.44						
L.S.D. at 5-percent level L.S.D. at 1-percent level	. 25 . 33	. 12	.0009	.05	. 14 . 18	. 03	, 3 8 ,51						

⁴The sum of the 6 individual elements is equal to the value listed, except for differences caused by rounding errors.

The pronounced effect of the first increment of magnesium in increasing leaf efficiency is an indication of the severity of magnesium deficiency at the low level of magnesium supply and offers a possible clue to a number of phenomena that have been observed with respect to magnesium nutrition both in this experiment and under field conditions. This increased leaf efficiency was the result of the combined effect of the first increased leaf efficiency was the result of the combined effect of the first increased leaf the same time it produced an increase in total dry weight of leaves only at the high level of potassium supply (table 5). The inefficiency of the leaves of the plants receiving the low level of magnesium may be accounted for by the short period for which each leaf remained on the tree after developing fully, as well as by the low magnesium content of the leaves. This short period of leaf activity, accompanied by the continuous development of new leaves, depleted the meager food-reserves available for feeding-root development to such an extent that feeding-root growth not only practically ceased, but the roots that were present deteriorated rapidly. At time of harvest, almost no live feeding roots remained on the plants receiving low magnesium. This reduction in feeding roots further decreased the absorption of magnesium as well as calcium and most of the minor elements. The effects of the three bases on feedingroot development are better illustrated by the ratios of stem-plus-storageroot weight to feeding-root weight than by feeding-root weights alone. The main factor controlling the ratio was the level of magnesium supply (table \$1, but both calcium and potassium altered the magnesium effect.

 TABLE S.—Main effects of 3 levels each of potassium, magnesium, and calcium and their interactions in yrams per plant on the ratio of dry weight of stems plus storage roots to dry weight of feeding roots

			Over-all											
Level		K-1			K-2			K-3		ef	effect of			
	('n-1	Ca-2	Ca-3	Ca-J	Ca 2	Ca-3	('a-1	('a-2	Ca-3	К	Mg	Ca		
Mg 1 Mg 2 Mg 3	Gm. 1.89 1.75 2.52	Gm. 1.87 2.22 2.25	Gm. 2.13 2.01 2.16	Gm. 2.71 1.95 2.45	Gm. 3.35 2.13 2.18	Gm. 6.32 2.09 2.31	Gm. 3.74 2.03 2.24	Gm. 5.30 2.08 2.51	Gm. 9.28 2.20 2.52	Gm. 2.09 2.83 3.54	Gm. 4.06 2.05 2.38	Gm. 2.30 2.65 3.45		

The first increment of magnesium reduced the ratio and the second increment increased it. The averages were 4.06, 2.05 and 2.38 at the Mg-1, Mg-2, and Mg-3 levels, respectively. The effects of potassium and calcium levels were nearly equal and both produced an increase in the ratio. This was merely a reflection of their effects on magnesium accumulation and function. The slight increase in the stem and storage root to feeding root ratio resulting from the second increment of magnesium (compare fig. 2, *B*, with fig. 2, *C*) was the result of an increase in storage-root weight in excess of the increase in feeding-root weight. This is a reflection of an increased efficiency of the feeding roots as well as of the leaves of the high magnesium plants, which permitted a greater accumulation of food reserves in the storage roots.

The increased production of feeding-roots resulting from the first increment of magnesium was undoubtedly responsible to a large extent for the accompanying increase in leaf content of calcium and a number of the minor elements.

Under field conditions, magnesium-deficiency symptoms on tung have not developed until late in the growing season. The data from this experiment would indicate that this may be caused by the production of feeding roots early in the spring from the little reserves present in the storage roots of magnesium-deficient trees. These feeding roots apparently are able to supply sufficient magnesium to maintain the foliage produced during the early part of the season, but as soon as the magnesium is depleted in the restricted feeding zone of the new roots magnesium-deficiency symptoms develop. On the other hand, this development of magnesium-deficiency symptoms may be the result of a change in the balance between the concentrations of potassium, magnesium, and calcium in the leaves. For, under normal conditions, there is a marked increase in calcium and a decrease in potassium, whereas the concentration of magnesium remains very much the same from early to late in the growing season.

The correction of magnesium deficiency in tung orchards, even with heavy and continued applications of magnesium sulfate, requires a number of seasons. The extremely poor feeding-root development accompanying magnesium deficiency is undoubtedly responsible for the difficulty in its correction.

Another outstanding and significant feature of the results of this experiment has been the effects of supply of potassium, magnesium, or calcium on the nitrogen content of the leaves, although there was no difference in nitrogen supply (tables 4 and 6). Increasing the magnesium supply in the substrate decreased the content of nitrogen in the leaves, the averages being 854, 767, and 745 m.e. per 100 gm. for the Mg-1, Mg-2, and Mg-3 levels, respectively (fig. 5). Potassium had a similar effect in that the average levels of nitrogen was 844, 762, and 760 m.e. per 100 gm., respectively, for the K-1, K-2, and K-3 levels. The effect of calcium was less pronounced, the over-all level of nitrogen being 825, 784, and 758 m.c. per 100 gm. for the Ca-1, Ca-2, and Ca-3 levels, respectively, even though the range of calcium in the supply was much greater than that of potassium or magnesium. Effects similar to those on nitrogen were obtained with respect to the phosphorus content of the leaves as a result of the different levels of potassium, magnesium, and calcium in the supply (tables 4 and 6; fig. 6).

These and other similar results of interactions make it obvious that studies of the effects of levels of one or more elements on growth and the accumulation of other elements conducted in factorial arrangements and in randomized complete block experiments are essential for maximum significant results.

As stated earlier, no one growth measurement can be arbitrarily selected as representative of the total response of the plant to environmental changes. From the numerous aspects of growth that were measured in the experiment herein reported, it is possible to evaluate the relative merits of the different measurements as valid criteria of response to nutritional changes.

All the growth measurements recorded were not affected to the same extent, and, in some cases, not even in the same manner by different treatments. There were, however, certain effects that were rather consistent. The most consistent and pronounced effect resulted from an increased supply of potassium, especially the first increment, which produced a large increase in every aspect of growth. The first increment of magnesium was also very effective in increasing most of the growth measurements, with the exception of leaf weight and number of nodes. These responses to the first increment of potassium and magnesium were to be expected, since the level of these elements in the leaves in the K-1 and Mg-1 treatments were so low (12.5 to 30.9 m.e. per 100 gm. for potassium and 3.9 to 10.4 m.e. per 100 gm. for magnesium) that they produced plants extremely deficient in either potassium or magnesium or both. The low levels of these elements were reflected not only by the reduced growth of the plants, as compared with those receiving higher levels of potassium and magnesium, but also by leaf symptoms, particularly those of magnesium deficiency.

An accurate quantitative evaluation of both magnesium- and potassium-deficiency symptoms on the leaves was impossible, because of the rapid leaf fall resulting from these deficiencies, particularly that of magnesium (fig. 1; table 5). For this reason, the best evaluation of the severity of magnesium deficiency is the percentage of total leaf weight dropped. This criterion of magnesium deficiency cannot be absolutely applied, however, since the plants receiving the low level of potassium combined with the medium and high levels of magnesium (table 5, treatments 4 to 9, inclusive) dropped higher percentages of their total leaf weight than did plants receiving the same amounts of magnesium and the higher levels of potassium. Since these plants showed no magnesiumdeficiency leaf pattern but did show mild symptoms indicative of potassium deficiency, it is reasonable to assume that leaf fall from these plants was caused by potassium deficiency. The only plants receiving the intermediate level of magnesium that showed any symptoms of magnesium deficiency were those receiving the high level of potassium (table 5, treatments 22 to 24) and those receiving the intermediate level of potassium and the high level of calcium (treatment 15), which showed only mild symptoms. The data in table 6 show that the magnesium content of the leaves from the plants that showed magnesium deficiency ranged from 3.9 to 17.0 m.e. per 100 gm, while plants that did not exhibit magnesium-deficiency symptoms had from 21.1 to 62.2 m.c. per 100 gm. of magnesium in the leaves.

The $\frac{K + Ca}{Mg}$ and $\frac{K}{Mg}$ ratios in the leaves were calculated from the leaf composition data, and, although not presented in detail, it is of interest that the $\frac{K + Ca}{Mg}$ ratio in the plants showing magnesium-deficiency symptoms ranged from 34.51 to 6.86, and in those showing no symptoms from 5.08 to 0.88. The $\frac{K}{Mg}$ ratios ranged from 19.64 to 2.23 and from 2.31 to 0.22, respectively, for the plants showing visible symptoms of magnesium deficiency and for those showing none. From these data it would appear that for magnesium the actual leaf content of the element was as good an indication of the deficiency level indicated by leaf symptoms as either the $\frac{K + Ca}{Mg}$ or the $\frac{K}{Mg}$ ratio. As not all possible ratios between the three bases were

tested in this experiment, this does not mean that, under all conditions, the actual level of magnesium will be a better index of the magnesium status of the plant than the ratio of magnesium to one or both of the other major bases.

A correlation of potassium deficiency with leaf composition is not so readily made, since the predominant effect of potassium deficiency was in limiting growth. Therefore, it is necessary to use the leaf composition as the basis for determining the cause of the limited growth. Plants receiving the low level of potassium and the intermediate or high level of magnesium made significantly less growth, judged by every measurement taken, than did plants receiving the same levels of magnesium and the higher levels of potassium (table 5). The leaves of plants receiving low potassium but adequate magnesium (treatments 4 to 9) were low in potassium only, the potassium contents ranging from 12.5 to 18.9 m.e. per 100 gm. (table 6). That the plants in the low-potassium, lowmagnesium treatments (1 to 3) were not potassium-deficient is evidenced by a potassium content of their leaves, which ranged from 28.5 to 30.9 m.e. per 100 gm.

If these data are compared with those for potassium in intermediatepotassium, high-magnesium treatments (16 to 18), which ranged from 26.0 to 31.7 m.e. per 100 gm, and which produced plants having total plant weights averaging almost three times those in treatments 1, 2, and 3. it is evident that this content of leaf potassium is adequate for good growth, provided all other nutrients are also in adequate supply. When low-potassium, low-magnesium plants (table 6, treatments 1 to 3) are compared with the intermediate-potassium, low-magnesium plants (table 6, treatments 10 to 12), it will be noted that the potassium content was approximately doubled, whereas the magnesium content was reduced to approximately one-half. When magnesium supply was increased to the intermediate level and potassium supply was at the second level (table 6, treatments 13 to 15), the leaf magnesium was increased four- or fivefold over that of treatments 10 to 12, but potassium in the leaves dropped to approximately the same level as that in the plants from the low-potassium, low-magnesium treatments. Growth, measured in any manner, was greatly increased in treatments 13 to 15, as compared with treatments 1 to 3 or with treatments 4 to 6, the lowpotassium, intermediate-magnesium levels. This is the result of maintaining a proper balance between potassium and magnesium while, at the same time, increasing the intensity of both,

Intensity of normal nutrition cannot be measured on the basis of the content of an element or of all elements per unit weight of the tissue, since plants receiving a properly balanced but inadequate level of nutrition will make only that amount of growth permitted by the limited level of supply. Tissue from such plants has approximately the same mineral content as that from plants receiving a higher level of properly balanced nutrients, even though the latter make much greater growth. For this reason, intensity of nutrition cannot be evaluated from leaf analysis alone but should be evaluated from the whole plant, where it is possible to measure total nutrient uptake, or by correlation of leaf analysis with total plant production.

The relatively minor effects on growth of a wide range in levels of calcium in this experiment are undoubtedly caused by a low calcium requirement — result of supplying one-fourth of the nitrogen in the ammonia form. In other experiments by the writers, data from which have not been published, it has been demonstrated that when one-fourth of the nitrogen is supplied as ammonia, tung trees, apparently normal in every respect, can be grown with as little as 12 m.e. of calcium per 100 gm. of dry leaf tissue.

Since, in this experiment, one-fourth of the nitrogen was supplied as the more readily assimilated ammonium ion, the nitrogen content was considerably higher than is usually found under field conditions or in sand culture receiving all nitrate nitrogen. Thus, though the treatments effected a wide range in leaf nitrogen, the nitrogen levels are not correlated with growth except indirectly, as they are related to levels of the bases that were correlated with growth. The effect of the bases in reducing leaf nitrogen (fig. 5) is undoubtedly caused by their competition with the ammonium ion for entrance into the plant (26). This explanation is emphasized by the effectiveness of potassium and magnesium in reducing leaf nitrogen. Though the reduction of calcium accumulation by the ammonium ion probably is accounted for chiefly by the effect of the ammonia on organic acid metabolism, as is pointed out on page 35 and page 42, the action of calcium on nitrogen accumulation is similar to that of potassium and magnesium.

The outstanding feature of the data on phosphorus content of the leaves (table 6; fig. 6, D to F) is the pronounced depressing effect of increasing levels of potassium. The effects of magnesium and calcium on phosphorus accumulation were different at different levels of one another and of potassium. No explanation for these effects is apparent, but that the inverse relationship between leaf content of potassium and phosphorus is a consistent phenomenon in tung seems well established on the basis of all of the data so far obtained by the writers. The same relationship has been found in numerous other experiments involving various levels and ratios of nitrogen, phosphorus, magnesium, and potassium, both under conditions of all-nitrate and under part-ammonia and partnitrate nutrition. Data from these other experiments (unpublished) lead to the conclusion that the high phosphorus in the leaves of the plants in the study reported here is the result of supplying one-fourth of the nitrogen as the ammonium ion. Leaves of plants grown on all-nitrate nitrogen and receiving a level of phosphorus equivalent to that supplied in this experiment have analyzed consistently lower in phosphorus. This ammonia-nitrate nitrogen relationship to phosphorus accumulation would indicate that the effect of the bases on phosphorus accumulation lies in the organic acid metabolism of the plant as affected by the ammonia-nitrate nitrogen ratio. Data from another experiment now in process of interpretation appear to support such an explanation.

The depressing effect of potassium on phosphorus accumulation has been reported for tung on field-grown material by Drosdoff and Painter (9) and on other species by Johnston and Hoagland (13) and by Colby (5).

RELATION BETWEEN THE POTASSIUM-MAGNESIUM-CALCIUM RATIO AND TOTAL ACCUMULATION OF POTASSIUM, MAGNESIUM, AND CALCIUM IN THE LEAVES

There is considerable evidence in the literature to support the general principle of antagonism between the bases. There is no doubt that, within certain limits, an increase in the supply of any one of the three major eations will cause an increased leaf content of that ion and a de-

crease in the leaf content of one or both of the two other cations. For this to be a consistent phenomenon, however, it would be necessary to have a constant milliequivalent accumulation of cations in the leaves under all nutritional conditions (14). Since the cation : anion ratio within the leaf must be a constant, the above conditions could only exist within a range of nutritional variations that would not materially affect the anion accumulation in the leaf. Further, since a considerable proportion of the anions present in the leaf are the products of organic synthesis, such as organic acid radicles, and since it has been shown by Pucher, Vickery, and Wakeman (21) and Pierce and Appleman (20) for other plants and by Gilbert, Shear, and Gropp (12) for tung that varying ratios of ammonia to nitrate nitrogen as well as varying ratios of potassium, magnesium, and calcium alter the organic acid content of the leaves, it is logical that the total cation demand would also vary. Furthermore, as a high percentage of the absorbed calcium is inactivated in many plants by precipitation as the oxalate and is, therefore, no longer able to affect materially the entrance of other cations, it might be expected that an increased calcium accumulation in such plants would affect an increase in the total cation accumulation in the leaf.

That calcium does exert such an effect on total eation accumulation is well illustrated by the total accumulation of calcium, magnesium, and potassium in the leaves of the plants in this experiment (table 6). The average effect of increasing calcium supply was to increase the total of the three bases, the data being 95.7, 130.4, and 164.3 m.e. per 100 gm. of dry leaf tissue for the Ca-1, Ca-2, and Ca-3 levels, respectively.

The interactions that occur between the three bases in their effect on total cation accumulation can be more readily visualized from an inspection of figure 12, that presents simultaneously the data for cation proportions in the leaves and total cation accumulation for each of the 27 treatments. This figure was constructed in the following manner: The calcium-magnesium-potassium units in the leaves calculated for each treatment are plotted on the plane surface by the method of trilinear coordinates described by Thomas (29) and Thomas and Mack (30). At the point on the triangle representing the calcium-magnesiumpotassium unit for each treatment the total of the milliequivalents of the three bases in the leaves is plotted in the third dimension, or perpendicular to the plane of the triangle. By this method it is possible to construct a solid figure having an upper surface, from the contour of which one is able to observe the effects of changes in the relative proportions in which the three elements accumulated on the total accumulation of the three.

The outstanding effect, as shown by the increased height in the calcium corner of figure 12, indicates that the greater the proportion of the total contributed by the calcium ion, the greater was the total accumulation. As the proportion of calcium to potassium and magnesium was reduced by the accumulation of either or both of the latter ions, the total cation accumulation was also reduced. The reduction in total cation accumulation, however, was not affected equally by potassium and magnesium. When magnesium was low and calcium was depressed by increased potassium accumulation, total cation accumulation was not reduced so markedly as when potassium was low and calcium was depressed by increased magnesium accumulation. Points representing all 27 treatments

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FIGURE 12.—A solid figure, showing the relationship between the composition of the Ca-Mg-K units (plotted on the plane surface of the triangle) and the total milliequivalent concentration of the three components of those units (plotted perpendicular to the plane surface of the triangle), as found in the dry matter of the leaves from tung trees grown in sand culture receiving nutrient solutions containing different ratios of calcium, magnesium, and pofassium.

are not visible in figure 12, because, at the extremely low levels of leaf magnesium in proportion to calcium and potassium (treatments 2, 3, 10 to 12), the total accumulation dropped precipitously, probably as a result of the very poor root development of these severely magnesiumdeficient plants. The points representing these treatments occur at the rear of the figure as viewed, and, though not visible, follow exactly the slope of the slightly higher magnesium treatments with increased potassium accumulation.

The increased leaf magnesium which resulted from increased calcium supply at the medium and high levels of magnesium combined with low potassium shows that this calcium effect in increasing total eation accumulation was partly the result of increased magnesium accumulation. The fact that this combined increase of calcium and magnesium did not materially affect potassium accumulation in the leaves indicates that the increased calcium and magnesium was in a nonionizable form, probably oxalate, which would not inhibit the accumulation of potassium in the leaves.

Data from other less extensive experiments indicate that the reduction of calcium accumulation by increased manganese (2S) results in a similar reduction in total cation accumulation.

This effect of calcium in increasing total cation accumulation is in agreement with the results of Mehlich and Reed (16) on cotton and of Albrecht and Schroeder (1) on spinach. Other investigators working with grass (31) and legumes (2) have not found this effect. It appears that cation equivalent constancy will occur only in those species producing no significant quantities of oxalic acid, whereas the relationship herein reported on tung would occur in oxalate-producing species.

Relation Between the Supply of Potassium, Magnesium, and Calcium and the Accumulation of Heavy Metals Plus Boron

Numerous investigators have noted relationships between the supply and accumulation of one or more of the bases on the accumulation in different plant parts of boron and certain of the heavy metals. Calciumboron relationships have been reported by Brenchley and Warington (3), Marsh and Shive (15), and Wolf (34). Potassium-boron relationships have been reported by White-Stevens (33), Purvis and Hanna (22), Reeve and Shive (23), and others. A magnesium-boron relationship in the nutrition of tung has previously been reported (27).

The depressing effects of potassium on manganese and copper accumulation in the leaves has previously been reported by the writers (28). Wallace (32) also found a similar potassium-manganese relationship, Reuther and Smith (24) have noted a similar relationship between potassium and zine in citrus.

Because of the marked effect of one or more of the bases on the accumulation of the heavy metals, it seems worth while to make a rather careful analysis of this phenomenon as revealed in the data presented. Potassium supply was the dominant factor, affecting not only the accumulation of potassium in the leaves but also that of boron and all of the heavy metals. In every case the potassium depressed the accumulation of the heavy metals and boron (table 7). It was also the major factor



FIGURE 13.—Relationship between potassium accumulation and the accumulation of the total of aluminum, boron, copper, iron, manganese, and zinc in the leaves.

influencing the accumulation of the total of all of these elements. In order to emphasize this relationship further the data for the potassium content in the leaves have been plotted against the leaf content of the total of the heavy metals and boron (fig. 13). A curvilinear relationship exists between the concentration of potassium in the leaves and the total concentration of heavy metals.⁴ Considering that there are nine different ratios of calcium to magnesium represented at each level of potassium and that both calcium and magnesium in the solution have been shown to influence the accumulation in the leaf of each of the minor elements, this close relationship takes on increased significance. Although potassium influences the amount of each of the heavy metals and boron that accumulates in the leaves in a slightly different manner and although calcium and magnesium also affect the leaf content of these minor ele-

- Coefficient of determination = 58.3 percent
- Regression equation Y = 10.902 0.0667X
- Sy. x = 1.262 m.e. /100 gm. dry matter of total heavy metals plus boron. Curvilinear regression:
 - Coefficient of correlation = -0.8081
 - Coefficient of determination = 65.3 percent
 - Regression equation $Y = 12.729 0.16998X + 0.01115X^2$
 - Sy. x = 1.156 m.e./100 gm, dry matter of total heavy metals plus boron.

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^{*} Linear regression :

Coefficient of correlation = -0.7632

ments, it appears from these data that there are compensatory interrelations between all of these ions which bring about this consistent relationship between potassium and the total of the heavy metals plus boron in the leaves.

The relationships between the supply of calcium or magnesium and leaf content of the heavy metals and boron do not appear at first glance to be consistent. Restated briefly, each of the two increments of magnesium produced a significant decrease in zinc, a significant decrease followed by a nonsignificant increase in boron, and an increase followed by a decrease in iron, manganese, copper, aluminum, and total heavy metals plus boron (table 7). The two increments of calcium resulted in a decrease in manganese, zinc, copper, and total heavy metals plus boron, an increase in iron, an increase in aluminum the first increment being followed by a nonsignificant decrease, and a decrease in boron followed by a slight increase (table 7).

The magnesium effect was consistent for all the heavy metals with the exception of zinc. There are two possible explanations for the increased content of iron, manganese, copper, aluminum, and total minor elements in the leaf, as well as of calcium, that resulted from the first increment of magnesium. Plants receiving the lowest level of magnesium had very poor root systems; the dry weight of feeding roots ranged from 0.58 to 6.32 gm. per plant. The few feeding roots produced on these plants deteriorated rapidly and probably functioned for only a short period. This poor root development may have been partially responsible for the low level of most of the cations in the leaves of these plants. Root development was greatly improved by the first increment of magnesium and may have been responsible for the increased leaf content of the cations at the Mg-2 level. The decreased leaf content of the cations at the Mg-3 as compared with the Mg-2 level may have been caused by cation competition that was able to function when normal root absorption was taking place.

The causes of the depressing effect of magnesium on zinc and the marked effect of the first increment of magnesium in reducing leaf boron are not readily apparent. It may be that the competitive effect of magnesium on these elements was of such a magnitude that it reduced the absorption of zinc with both increments and of boron with the first increment; however, the second increment of magnesium resulted in no significant change, notwithstanding the beneficial effects of the increased feeding-root efficiency.

The other possible explanation is that the greatest decrease in leaf potassium resulted from the first increment of magnesium. Since it has already been shown that leaf potassium was inversely correlated with content of the heavy metals and boron in the leaf, it would be expected that the reduced potassium content resulting from the increased magnesium would bring about an increased accumulation of these elements.

Although the second increment of magnesium produced a large increase in leaf magnesium, it was not accompanied by an equivalent decrease in potassium (fig. 9). Thus, the effect of the second increment of magnesium on the heavy metals and boron would be predominantly the competitive effect of increased magnesium rather than that of decreased potassium and would result in the observed reduction of the heavy metals and no further decrease in boron. This second explanation seems the more logical, particularly in view of the effects of calcium on the minor elements.

With the exception of iron and aluminum, the heavy metal and boron content of the leaves was reduced by calcium. As calcium accumulation only slightly affected potassium content of the leaves (fig. 10) and either produced only a slight effect or a marked increase in magnesium content, it would be expected, on the basis of cation competition, that the increase in leaf calcium and magnesium in response to increased calcium supply would result in a decreased accumulation of the heavy metals and boron.

The increase in content of iron and aluminum in the leaves resulting from increased calcium may have been caused by the inactivation in nonionizable form of these two metals as a result of an increased oxidation potential brought about by the increased calcium accumulation. Data indicating such a response to increased calcium have been obtained by coworkers on tung (12).

It thus appears that when the supply of any one or all of the heavy metals and boron is held constant, the controlling factor affecting their accumulation in the leaves is the level of potassium supply and consequent level of leaf potassium. This potassium effect dominates the effects of calcium and magnesium to such an extent that only when leaf potassium is just slightly affected by rather large variations in leaf calcium and magnesium can these latter cations exert their individual or combined competitive effect- on the accumulation of the heavy metals and boron.

RELATION BETWEEN THE ACCUMULATION OF POTASSIUM, MAGNESIUM, AND CALCIUM AND THE ACCUMULATION OF SODIUM IN THE LEAVES

The r -acity of the plant to absorb or reject the sodium ion varies with different species. In the species that readily absorb sodium, the interactions between sodium and the other cations are very similar to those already described for potassium (∂t) . In such plants, sodium, though not an essential nutrient element, may act as an important factor in nutrition through its effects on the accumulation of the nutrient cations, especially potassium, and the balance between them.

Although the tung tree tends to reject sodium and the sodium accumulation in the leaves in this experiment bore no relation to the level of supply, the effects of other major eations on leaf sodium were significant. Sodium accumulation was greatly increased by increasing potassium supply, but calcium and magnesium also had important effects. The first increment of magnesium increased sodium accumulation, but the second increment greatly reduced it. On the other hand, the first increment of calcium decreased sodium accumulation but the second increment resulted in no further change. Notwithstanding these effects, the level of potassium supply had the outstanding effect of increasing both potassium and sodium accumulation in the leaves, the very highly significant linear coefficient or correlation being +0.7361. The regression equation was Y = 72.277 N = 10.234, and Sy, x = -3.22 nucl of potassium per 100 gm, of dry matter. The coefficient of determination of 54.18 percent is quite remarkable, as it indicates that most of the sodium accumulation in the leaves was determined by the accumulation of potassium in them. This relationship is opposite to that of the other cations with potassium.

which indicates that the effect of potassium on sodium is not one of competition.

Since sodium absorption is evidently selectively inhibited by the roots of the tung tree, one would not expect its uptake to be affected in a competitive manner by other cations. However, any alterations in root permeability resulting from variations in the composition of the nutrient solution would be expected to be reflected in altered sodium uptake. The direction of the effects of potassium, magnesium, and calcium supply on sodium accumulation in this study fits such an hypothesis. It is generally recognized that the monovalent cations, especially potassium, increase protoplasmic permeability, whereas the bivalent cations decrease permeability. Thus, the increased sodium uptake that accompanied increased potassium supply and decreased magnesium and calcium supply could very possibly be caused by altered protoplasmic permeability.

VARIOUS GROWTH MEASUREMENTS AS CRITERIA OF RESPONSE TO NUTRITIONAL TREATMENTS

Of the numerous growth measurements recorded on the plants in this study, no one alone gave a complete picture of response to nutritional treatment. Total plant weight by itself, for example, gave a false picture of the effect of potassium in increasing magnesium deficiency. A comparison of the total plant weight in the K-1 plus Mg-1 treatments with those in the K-2 plus Mg-1 and K-3 plus Mg-1 treatments (table 5) indicated that the greatest weight was at the second level of potassium. The weight at the third level of potassium was intermediate between that at the first and second levels. Inspection of the data for total weight of leaves produced, however, shows that most of the increased plant weight resulting from the increased potassium was caused by increased leaf weight. Since the increased magnesium deficiency resulting from the higher levels of potassium caused an increased leaf drop, the greater leaf weight was not accompanied by increased stem and root weight, but, especially at the high level of potassium, produced a large decrease in stems plus roots. This was owing to the greatly lowered leaf efficiency under conditions of high potassium and low magnesium,

Even though leaf fall was not significantly different at the Mg-2 and Mg-3 levels within a given level of potassium, leaf efficiency was, nevertheless, higher at the third than at the second level of magnesium at all levels of potassium supply. This would indicate that photosynthesis was improved by the further increase in magnesium, although visual magnesium-deficiency symptoms were not usually present at the Mg-2 level.

The mode of action of each one of the major bases in affecting plant beight is shown by the two growth phenomena, the number of nodes and the length of internodes. Increases of both potassium and magnesium resulted in increased plant height (fig. 3, A and F). Increasing calcium, however, decreased plant height. Although potassium and magnesium both increased plant height, their effects on number of nodes were directly opposite (fig. 3, E). Both increments of potassium greatly increased number of nodes, whereas both increments of magnesium reduced number of nodes; the effect of the first increment being the greater With the exception of the second increment at the low level of magnesium, potassium increased the length of internodes (fig. 3, B). From this it can be seen that increased height resulting from the higher levels of potassium was caused by the increased number of nodes. All increase in height resulting from magnesium increments, however, was caused by the greater length of internodes. The reduced height brought about by calcium was entirely the result of decreased length of internodes.

As far as the writers are aware, there are no other data on the effects of nutrition on the specific gravity of wood. From the results presented, it can be assumed that the magnesium nutrition of the tung trees was a dominant factor affecting the specific gravity of the wood. Histological studies are under way on stem samples from the trees produced in this experiment and should make possible an explanation of these differences in specific gravity on a morphological basis.

In any tree crop structural strength of the wood is important. In tung, which bears heavy crops of fruit and is grown in an area subject to severe windstorms, this factor has added importance. Any information that may contribute to our knowledge of the factors affecting structural strength of the trees has great practical application.

Use of Leaf Analysis in the Interpretation of Nutritional Status and Growth Response

Numerous attempts have been made at mathematical expression to represent the relationships between the supply of various elements and their accumulation in different plant parts and between the ratios of certain elements in the plant and various aspects of growth and fruiting. So far, these mathematical expressions have not found wide application. In the results of the experiment herein reported may be found the explanation for the lack of success in such attempts as well as an indication of some of the factors that must be considered in attempting to formulate such mathematical relationships.

The data reported in this bulletin have demonstrated that the concentration of any given element in the leaves is a function, not alone of the concentration of that element in the supply but also of the concentration of that element in relation to that of every other element in the supply and the consequent accumulation of all other elements in the leaves and their resultant effects on metabolism and growth. The aspects of these relationships have already been stated by the writers in their concept of nutrient-element balance (27).

Were it necessary to integrate only the effects of varying ratios of supply of calcium, magnesium, and potassium on the accumulation of one another in the leaves and to interpret growth responses in terms of these three elements alone, the problem would be complex. But when the effects of the accumulation of these elements on the accumulation of all of the other elements are recognized, the problem is even more complex.

The effects of the bases on the heavy metals and boron accumulation illustrate well the difficulties of interpretations of foliar analysis, even when analyses include all of the known essential elements, and should indicate the impossibility of interpretation on the basis of only the socalled major elements.

In this experiment the elements other than the three major cations

were supplied in concentrations sufficient to prevent their concentrations in the leaves from dropping to levels that would materially reduce growth, even under the conditions most unfavorable for their uptake. Had the heavy metals and boron, for example, been so low in the supply as to become critically deficient under conditions of high potassium accumulation, any interpretation of the effects of potassium on growth would have necessarily become impossible, since the effects contributed by the resulting change in the accumulation of each of the heavy metals and boron could not have been evaluated.

These observations do not mean that leaf analyses cannot be profitably used to interpret the nutritional status of plants. On the contrary, leaf analyses, in conjunction with a fairly complete evaluation of soil and other environmental conditions and with fairly full information on tree growth and fruiting performance, are being widely used to great advantage by tung growers and others.

Such indications of complex nutritional relationships as have been illustrated in the study serve to make the investigator aware of the factors that must be considered and to prompt further investigation in an attempt to clarify the relationships so far recognized and to uncover further relationships that may exist.

SUMMARY

The effects of varying levels and ratios of calcium, magnesium, and potassium on the growth and mineral composition of the leaves of seedling tung trees grown in sand culture were studied in an experiment having a complete block design of four replications and involving a 3 by 3 by 3 factorial arrangement of the above-named cations.

The results show that each of these 3 elements have a highly significant primary effect us well as interactions on all criteria of tree growth and on the accumulation of the 12 elements studied.

The bearing of the results of this experiment on the interpretation of leaf analyses are discussed. It is emphasized that the primary effects and complex interactions between the level of supply of the various elements and their effects on leaf composition and growth do not invalidate the use of leaf analyses as a means of determining nutritional status of plants, but rather demonstrate the importance of a more complete understanding of these phenomena in order to increase the value of foliar analysis.

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