PHOSPHORUS AND NITROGEN METABOLISM IN SOYBEANS AS INFLUENCED BY POTASSIUM.

by

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INTRODUCTION

The importance of potassium in plant nutrition has long been recognised. However, the specific metabolic role(s) of potassium in plant growth has not been clearly elucidated. It has been suggested that potassium regulates such diverse processes as respiration, photosynthesis, carbohydrate synthesis and degradation, protein synthesis, chlorophyll formation, and translocation of starch.

It is difficult to elucidate the metabolic role of potassium because of its general effect on many biochemical processes occurring within plants. Potassium can affect such diverse pathways as protein synthesis and carbohydrate metabolism by its influence on the synthesis or metabolism of an intermediate common to both pathways. An intermediate common to both systems is adenosine triphosphate (ATP) and related phosphate compounds.

Any ion which directly or indirectly affects phosphate metabolism can greatly alter such important pathways as protein synthesis and carbohydrate metabolism. Therefore, a study of the effect of potassium on general phosphate metabolism coupled with a similar study of nitrogen metabolism, may give some insight into the possible regulatory role of potassium in plant metabolism.

Soybean seedlings, Glycine max, used for this research normally have relatively high contents of potassium, phosphorus, and nitrogen, ions that were studied in detail. In addition;

soybean plants grow relatively rapid and are well adapted to greenhouse conditions, making it an excellent indicator plant.

The main objectives of this study were as follows:

1. To determine a possible function(s) of potassium in plant growth or metabolism.
2. To investigate the hypothesis that potassium is a cofactor in phosphorus metabolism.
3. To measure, if possible, the minimum and maximum concentrations of potassium required for "normal" phosphorus and nitrogen metabolism.

LITERATURE REVIEW

Each mineral nutrient required by plants, if deficient, causes one or more external and/or internal abnormality. Potassium is a macronutrient or macrometabolic element found in plants in amounts often exceeded only by carbon, oxygen, hydrogen, and nitrogen.

Potassium is absolutely essential to plants and cannot be replaced entirely by another element. In view of this and because of the large amount needed by plants, it seems almost incredible that the specific role of potassium in growth processes has never been fully elucidated. In spite of extensive research, potassium remains an element of mystery insofar as its function in living tissue is concerned. Only by noting the effects of its absence on a plant has its role been deduced (Gilbert, 1957).

Potassium Requirement for Plant Growth

Critical potassium content

The reported critical potassium content (per cent dry weight) required for normal growth varies with plants and authors. Gerwig and Ahlgren (1958) found the critical percentage to vary from season to season, but probably lies within the range of 1.42 to 1.84 per cent. McNaught (1958) reported the critical level for near-maximum growth for white and red clover leaves to be 1.8 per cent potassium. He also reported the level to be approximately 1.6 per cent for ryegrass, orchardgrass, and Yorkshire fog. Many plants that contain one per cent or less potassium show rather severe potassium deficiency symptoms (Kresge and Younts, 1960 and Stivers and Ohlrogge, 1952).

Distribution of potassium in plants

Potassium distribution is not uniform in plants. When deficiencies occur, potassium is concentrated in the newly-developed plant parts (Black, 1957). With ample potassium supplies, the concentration may be greater in older than in the younger tissue (Bowling and Brown, 1947). Microchemical studies indicate that potassium occurs in the cytoplasm and vacuoles, but not within the nucleus (Macallum, 1905 and Penston, 1931). Gamble (1962), working with rat liver mitochondria, found that potassium behaves as though it was contained at a relatively fixed concentration, close to 90 meq/l.

Deficiency symptoms

Potassium deficiency usually is first manifested by a yellowing of the tips and edges of older lamella or leaflets. As deficiencies become more severe, the yellowed areas progress toward the center and base of the leaves. In advanced stages of potassium starvation, the leaf edges become necrotic and the tissue disintegrates (Lawton and Cook, 1954). In some instances with initial potassium deficiency the leaves are dark green or bluish-green in color (Black, 1957).

Function of Potassium in Plants

General metabolic role

Literature on the metabolic role of potassium has been summarized by Black (1957). He reported that the potassium content of plants is positively correlated with the rate of metabolism. Potassium appears to be required for at least two different metabolic reactions, in carbohydrate as well as nitrogen metabolism.

Pirson (1955) stated that the potassium level of the cell controls the processes of photosynthesis and respiration to a high degree, and the magnitude of these metabolic processes is associated with potassium uptake. Humbert (1963) indicated that potassium affects transpiration, carbohydrate metabolism, protein synthesis, enzyme activity, meristem growth, stomatal movement, and water relationships in plants as well as photosynthesis and respiration--all important for optimum plant growth.

Carbohydrate metabolism

Potassium deficiencies have been found to both increase and decrease the level of carbohydrates in plants (Wall, 1939). Environmental conditions, severity of deficiency, plant tissue analyzed and supply of other nutrients markedly influence the carbohydrate status or level observed in potassium deficiency. Wall (1939) attributed the initial carbohydrate accumulation under potassium deficiency to a "mass action" effect resulting from reduced protein synthesis. He also stated that carbohydrates generally decrease in severe and long-standing potassium deficiency. Eaton (1952) reported similar results with sunflower plants.

Ward (1959) working with potatoes reported the starch content of the leaves was a direct function of the amount of potassium applied, but the starch content of the tubers was not. The plant part most seriously affected by potassium deficiency was the leaf tissue where carbohydrates are synthesized and the end product, starch, reflected the disorder (Ward, 1959).

The role of potassium in carbohydrate metabolism may be indirect rather than direct. Potassium may be required early in the general metabolic pathway and when a deficiency of potassium exists one or more reactions may be blocked causing an initial increase then a decrease in the carbohydrate level (Gauch, 1957). Hoagland (1948) states, "When plants are grown for a long period under potassium deficiency, carbohydrate synthesis and metabolism will be affected, no matter what the essential function of potassium may be".

Nitrogen metabolism

The hypothesis involving potassium in a direct relationship to nitrogen metabolism suggests that organic nitrogen fractions are increased as a result of a disturbance in protein synthesis (Lawton and Cook, 1954). Wall (1939, 1940) and others have attributed the initial accumulation of carbohydrates in the early stages of potassium starvation to this hypothesis. It was also pointed out that proteolysis does not occur at a high rate if abundant carbohydrates are present, thus eliminating protein breakdown as the primary source of the increased soluble organic nitrogen fraction.

Richards and Coleman (1952) reported that the accumulation of putrescine (1,4-diamino-butane) occurred under potassium deficiency in barley seedlings. Similar symptoms were induced when putrescine was administered to plants with an adequate potassium supply. The accumulation of putrescine, however, was not always found with potassium deficiency (Coleman and Richards, 1956). Recent work by Smith (1963) indicates that the accumulation of putrescine and related amines (agmatine) under potassium deficiencies is due to the enhanced arginine decarboxylase activity. Griffith et al. (1960) reported an accumulation of amide nitrogen (mainly asparagine) under high nitrogen-low potassium fertilization of orchardgrass, which indicated abnormal nitrogen metabolism.

Amino acid incorporation into proteins by pea seedling preparations has been shown to require adenosine triphosphate (ATP), magnesium and a monovalent cation (Webster, 1959). The monovalent cation, potassium, markedly enhanced the amino acid incorporation into proteins. He further indicated that the enhanced amino acid incorporation specifically by potassium ions was similar to the necessity of the same ion (K^+) for the synthesis of simple peptides. The monovalent cations, Na, Li and NH_4 had little effect and Rb ions were inhibitory. Webster concluded that the observed enhancement of protein synthesis in potato disks and bacterial protoplasts by the potassium ion may be a reflection of a necessity of potassium for the formation of peptide bonds of protein molecules.

Potassium has been implicated in the synthesis of several enzymes (Thomas, et al., 1959 and Ward, 1959), and in the biosynthesis of nucleic acid bases, adenine, guanine and uracil (Okuda and Nakamigawa, 1958). Potassium can not be replaced by any other monovalent cation in the biosynthesis of these nucleic acid bases (Okuda and Nakamigawa, 1958).

Phosphate metabolism and enzymatic activity

Luev and Golubeva (1960), working with wheat sprouts, stated that potassium deficiencies do not appreciably affect the relative distribution of phosphorus in its various fractions. Potassium deficiencies caused sharp reductions in phosphorus movement from the roots into the plants, and general phosphorus metabolism was severely disrupted. It also caused a severe drop in the absolute content of organic-phosphorus, especially in compounds containing both nitrogen and phosphorus. Kotyk (1958) suggested that potassium was required for the phosphorylation of endogenous substrate by regulating the incorporation of inorganic phosphate into the structural components. Pressman and Lardy (1955) stated that potassium is required in reactions closely allied with esterification of inorganic phosphate. They concluded that potassium participates in transphosphorylation reactions, but does not directly influence the oxidative reactions.

Hartt (1934) observed that potassium deficient plants showed a reduced invertase and increased amylase activities. Potassium has been established as an essential activator for pyruvate kinase (ATP-pyruvic transphosphorylase), aceto-Co.A.-kinase, phosphotransacetylase and fructokinase (Fruton and Simmonds, 1958 and Lardy, 1951). The potassium activation of acetylation reactions has been explained in terms of the potassium requirement of each of the two known pathways for acetate activation by ATP. (Pressman and Lardy, 1955).

Lardy (1951) reported that "one generalization which seems to be justified is that the specific requirements for divalent cations are met by rather low concentrations, while the monovalent cation (K) is, in many cases required in relatively high concentrations". Gauch (1957) stated that this generalization by Lardy (1951) might explain the need of a high concentration of potassium.

Photosynthesis

According to Rabinowitch (1945), potassium deficiency causes chlorosis (insufficient development of chlorophyll) and therefore a depressed rate of photosynthesis. He further reported "that in addition to this indirect effect, potassium has also a direct effect on photosynthesis, since an addition of this element to the medium may cause an immediate increase in the rate of photosynthesis". Pirson (1955) also concluded that the potassium ion has a direct effect on photosynthesis.

Latzko (1959) postulated that the role of potassium in photosynthetic phosphorylation is similar to that of magnesium. This has not, however, been confirmed. Okuda and Nakamigawa (1958) have also reported a specific requirement for potassium in photosynthesis. Osbun et al. (1963) working with bean plants reported that potassium deficiency slightly reduced carbon dioxide fixation (uptake) and oxygen evolution in both light and darkness. Respiration, however, was increased by potassium deficiency both in light and darkness.

EXPERIMENT I

PROCEDURES

Physical and Cultural Conditions

Establishment

Soybeans (*Glycine max*, Var. Dorman) were seeded uniformly in the greenhouse on February 5, 1963 in two flats filled with 8-mesh white quartz sand.[1] The seedlings were grown for 20 days with a 5X dilution of complete Hoagland's solution (Hoagland and Arnon, 1938) applied at ten days to maintain satisfactory growth. Six seedlings were then transplanted into 2-gallon plastic containers filled with the 8-mesh white quartz sand. After a five day equilibration period, the pots were thinned to five plants. The seedlings were in the first trifoliate leaf stage of development at this time. Just prior to imposing the fertility levels, the cotyledons were removed from all seedlings to eliminate these as a possible potassium supply. Flower initiation was avoided by providing supplementary light to obtain approximately a 16 hour photoperiod.

Culture system

The culture drainage system consisted of a 2-foot section of ¼ inch plastic tubing with a 2-inch section of capillary tubing inserted in the end to restrict the drainage flow rate. The solution drained into a 1-gallon black reservoir. The sand

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[1] Obtained from Pennsylvania Glass Sand Corporation, size 4Q-ROK.

containers were irrigated or flooded manually every three to five hours with three liters of the nutrient solution. The frequency of irrigation was adjusted to the prevailing rate of transpo-evaporation.

Nutrient solution

The basic nutrient solution used was Hoagland and Arnon's minus K solution, second method of substitution (Hoagland and Arnon, 1938). The solution contained the following nutrients (g/l): $Ca(NO_3)_2 \cdot 4H_2O$, 1.181; $MgSO_4 \cdot 7H_2O$, 0.493; $Ca(H_2PO_4)_2 \cdot H_2O$, 0.1261; H_3BO_3, 0.0025; $MnCl_2 \cdot 4H_2O$, 0.0018; $ZnCl_2$, 0.0001; $CuCl_2 \cdot 2H_2O$, 0.00005; and MoO_3, 0.00008. Iron was supplied in the chelated form as Fe-EDTA[2] at the rate of .036 ml/l of 5% Fe. Potassium was supplied as KCl at the rates indicated below:

ppm K	gms. KCl/l of nutrient solution
0	none
20	0.0381
40	0.0762
80	0.1524
160	0.3048

In all cases the nutrient solution was renewed at weekly intervals. A small aliquot of each fresh solution was taken immediately after preparation for pH determinations. Just prior to discarding the solution from the individual pot reservoir (after one week), the solution was reconstituted to approximately three liters and an aliquot taken for subsequent

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[2] Versenol from Dow Chemical Company, Midland, Michigan

pH determination.

Experimental design

The experiment was arranged as a split-plot design with harvest dates as the main plot and potassium nutrition levels as the sub-plots in each of three replications. At weekly intervals, one complete pot (five plants) was harvested from each replication of the five potassium nutrition levels. The plants were cut just above the point of the cotyledonary node at each harvest.

Biochemical Determinations

After harvesting, the plant material was placed in a cold chamber, taken to the laboratory and washed three times with a cold dilute $CaCl_2$ (0.01%) solution and immediately frozen. The plant material was then lyophilized, after this it was weighed, ground in a micro-Wiley mill to pass a 40-mesh screen, and stored over P_2O_5 in a vacuum desiccator at approximately 0° C. One gram of the soybean tissue material was then fractionated as follows (Baker and Schmidt, 1963): 1. An initial extraction with 10% trichloroacetic acid (TCA) at 0° C. for 10 minutes, followed by three similar extractions with 5% TCA to remove the acid-soluble phosphate and nitrogenous compounds. 2. The TCA, phospholipid, and lipo-nitrogen compounds were removed from the residue by two extractions with 95% ethanol (ETOH) at 0° C. for one hour followed by four extractions with ethanol-ether (3:1, v/v) for 20 minutes at 45° C. 3. The nucleic acids were extracted from the lipid-free residue with 1N KOH for 60 minutes at 37° C.

The phosphate components of the cold TCA extract were separated using one gram Norit-A (activated charcoal) columns (1.5 cm x 2 cm). Immediately before adding the extract, the Norit-A column was washed with 10 ml of cold distilled water then 10 ml of cold 10% TCA. With the procedure of Baker and Schmidt (1963) the cold TCA fraction was separated into orthophosphate, organic phosphates and Norit-A adsorbable phosphates. The 1N KOH extracts were adjusted to approximately pH 6.5 with HCl before subjecting these to any analysis.

Phosphate was determined colorimetrically at 660 mμ in a B & L "Spectronic 20" spectrophotometer using the method of Fiske and Subbarow (1925). Total N (reduced-N) was determined for each of the extracts with the modified micro-kjeldahl procedure described by Schmidt (1961). A Beckman model DU flame spectrophotometer was used to determine potassium.

RESULTS

The three replications were combined to obtain enough plant tissue for analysis. Therefore, only the dry matter data have been subjected to statistical analysis.

pH of the Nutrient Solution

The pH values of the fresh nutrient solutions ranged from 6.2 to 6.5, Table 1. The variation in pH was greater between weeks than among K levels within a week. No consistent trends in pH due to K levels were noted at the end of one week. The somewhat high values for the fourth harvest date (28 days) may have been due to the exudation of organic acids from plant roots and also a higher uptake of cations from the nutrient solution.

Table 1. pH of the Nutrient Solution Initially and One Week Later

K^+ Added	Harvest Date (Days After K^+ Treatment)							
	7		14		21		28	
ppm	Initial	Final	Initial	Final	Initial	Final	Initial	Final
0	6.4	7.4	6.5	7.0	6.4	7.0	6.4	7.4
20	6.3	7.4	6.5	7.0	6.4	7.0	6.4	7.7
40	6.2	7.3	6.5	7.0	6.4	7.0	6.4	7.6
80	6.2	7.3	6.4	7.0	6.3	7.1	6.4	7.6
160	6.2	7.2	6.5	6.9	6.3	7.0	6.4	7.6

Dry Matter Yield

There was no difference among the applied K levels with respect to the overall mean for each level. However, the yield for all K levels was greater than the minus K treatment. The total mean yield was significantly greater for each successive harvest date.

The highly significant interaction indicates that the yields from added potassium changed among the harvest dates. Partitioning of the interaction (Appendix 1) to the response of potassium within each harvest, showed that essentially all of the yield response due to potassium occurred at the 28-day harvest. The different K levels showed no significant effect at the 7, 14, or 21-day harvests. This was probably a reflection of the endogenous K supply. The minus K treatment at 28 days was significantly lower than any of the applied potassium levels.

From these data, it may be concluded that soybean seeds supplied enough potassium for growth for approximately 21 days after adding the K treatments (a total of 46 days, 25 days establishment + 21 days).

Total yield increased exponentially with time, Figure 1. This has been plotted in the Log form and throughout this manuscript will be referred to as a logarithmetic effect. The rate of increase (slope of the line) was somewhat less for the minus potassium treatment than for the various added potassium levels. This difference is attributed to the significant interaction.

There was a slight deviation from the logarithmic increase at the 7-day harvest. This may have been due to a mild "shock-effect" from the abrupt change in the root environment. From germination until day-0, a period of 25 days, the plants were grown in sand with only water. At day-0, the nutrient solutions were applied, thus the salts plus the change in osmotic pressure may have reduced growth. Therefore, after a short equilibration period, the increase in dry matter with time was logarithmic.

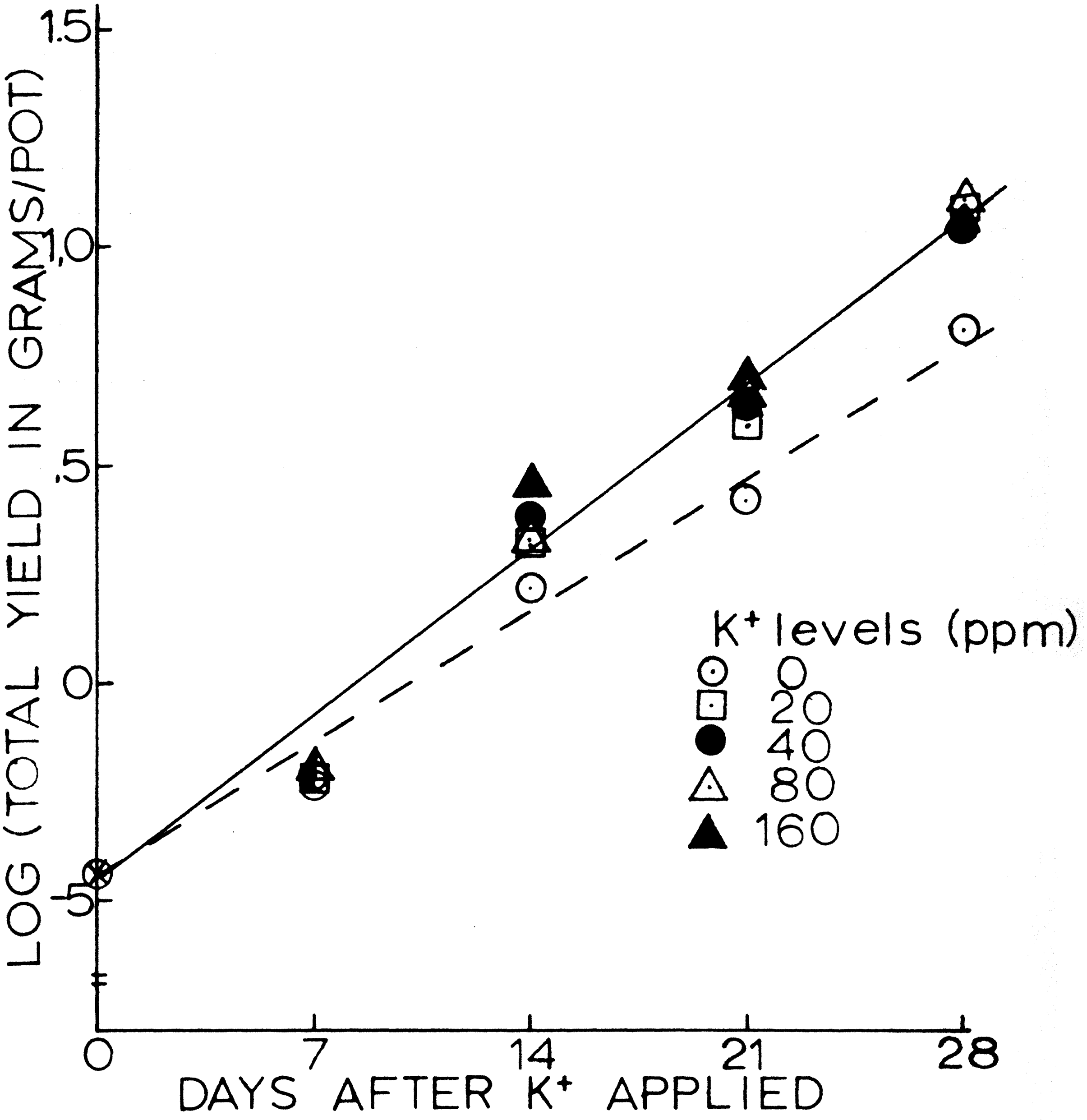

FIGURE 1. YIELD INCREASE AS INFLUENCED BY TIME AND K^+ NUTRITION.

Table 2. Dry Matter Yield as Influenced by Potassium and Time (g./plant)

K^+ Added (ppm)	Days After K^+ Added				
	7	14	21	28	Mean
0	.114	.337	.617	1.209a*	.569a*
20	.115	.379	.738	2.299cd	.883b
40	.115	.435	.789	2.178bc	.878b
80	.117	.407	.880	2.467d	.968b
160	.128	.517	.780	1.995b	.855b
Mean	.118	.415	.760	2.030	

*Values in the same column not having the same letter differ significantly at the 1% level.

Chemical Composition and Nutrient Uptake

Potassium

The potassium percentage increased with increasing amounts of added K, Table 3. The potassium content at the 160 and 80 ppm levels was similar throughout the four weekly harvests. With the 40 ppm level a decrease in potassium percentage of plants occurred after the second week. The plants grown with 0 and 20 ppm K levels decreased in potassium content with advancing age.

The per cent potassium as influenced by K level and age is shown in Figure 2. When the potassium content was below 1.60%, deficiency symptoms were detectable. Slight potassium deficiencies (yellowing of the older leaf tissue) were noted at 14 days for the minus K level. At 21 days the 0 and 20 ppm levels showed mild and slight deficiencies respectively.

Table 3. Potassium, Phosphate, and Nitrogen Content and Uptake as Affected by Age and Potassium Nutrition.

Harvest Date	K^+ Added	Nutrient Content			Nutrient Uptake			Yield (Dry Wt.)
		K	P	N	K	P	N	
Days after K^+ added	ppm	%	%	%	mg/pot	mg/pot	mg/pot	g/pot
0	0	1.76	.5409	4.28	6.51	2.00	15.84	0.370
7	0	1.10	.6040	4.11	6.27	3.44	23.43	0.570
	20	1.65	.5682	3.00	9.52	3.28	17.31	0.577
	40	1.27	.5797	4.05	7.33	3.35	23.37	0.577
	80	2.36	.5118	4.58	13.76	2.98	26.70	0.583
	160	3.10	.5654	3.84	19.78	3.61	24.50	0.638
14	0	1.00	.7355	3.75	16.75	12.32	62.81	1.675
	20	1.60	.5852	3.69	33.52	12.26	77.31	2.095
	40	2.62	.5919	4.21	63.01	14.24	101.25	2.405
	80	2.96	.5624	3.81	62.31	11.84	80.20	2.105
	160	3.44	.5416	3.31	104.23	16.41	100.29	3.030
21	0	0.46	.7435	4.50	12.08	19.52	118.12	2.625
	20	1.32	.5424	3.81	51.81	21.29	149.54	3.925
	40	2.34	.5284	4.09	101.79	22.98	177.92	4.350
	80	2.80	.5180	3.64	128.80	23.83	167.44	4.600
	160	3.52	.5195	3.93	180.40	26.62	201.41	5.125
28	0	0.26	.7841	4.01	17.13	51.67	264.26	6.590
	20	0.92	.4840	3.25	114.49	60.23	404.46	12.445
	40	1.64	.4332	3.45	181.22	47.87	381.22	11.050
	80	2.24	.4470	3.05	291.65	58.20	397.11	13.020
	160	3.16	.4321	3.22	369.72	50.57	376.74	11.700

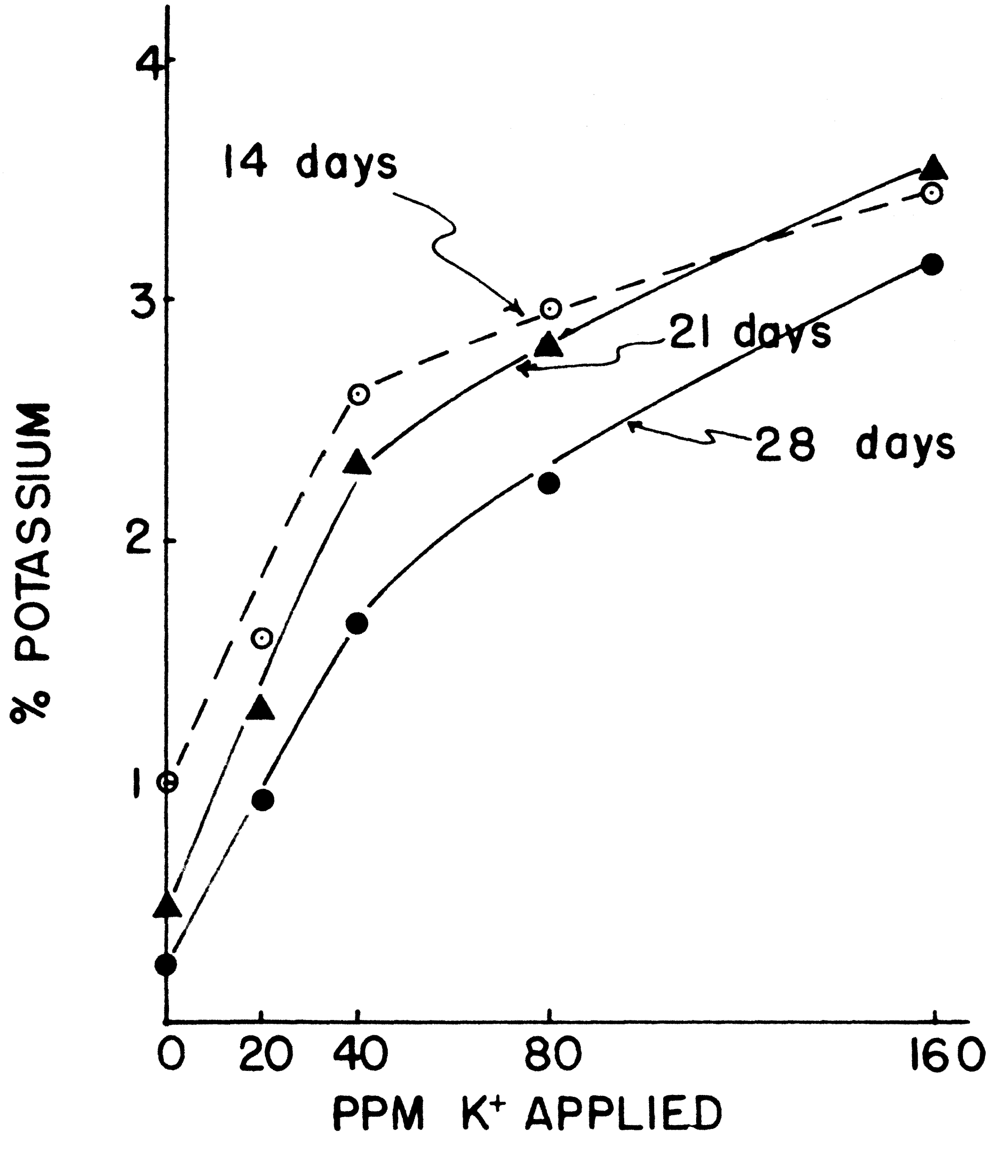

FIGURE 2. POTASSIUM CONTENT AS INFLUENCED BY K^+ NUTRITION AND AGE.

After 28 days the plants at the 0 level showed marked potassium deficiency (0.26%K), the 20 ppm level showed a mild deficiency (0.92% K), whereas the 40 ppm level (1.64% K) exhibited traces of a deficiency.

Phosphorus

The per cent phosphorus of the leaves generally decreased with increased amounts of K. Phosphate uptake increased logarithmically with time, Figure 3. There was no apparent relationship between K levels and phosphate uptake. The slight deviation of phosphate uptake at seven days may be a reflection of the initial equilibration of the plant roots when nutrient solutions were applied.

Nitrogen

There appears to be a general trend for the nitrogen percentage to decrease with increasing K levels, Table 3. This effect was much less pronounced than for phosphorus content. The high nitrogen content for minus K is probably a concentrating effect resulting from the lower yield.

There appears to be a positive relationship between nitrogen uptake and level of potassium, Table 3. Nitrogen uptake generally increased logarithmically with time, Figure 4. The slope of the line for nitrogen uptake for minus K is somewhat less than that for the four K levels. No differences were detectable among the four different K rates. The difference in the two indicated slopes could be interpreted

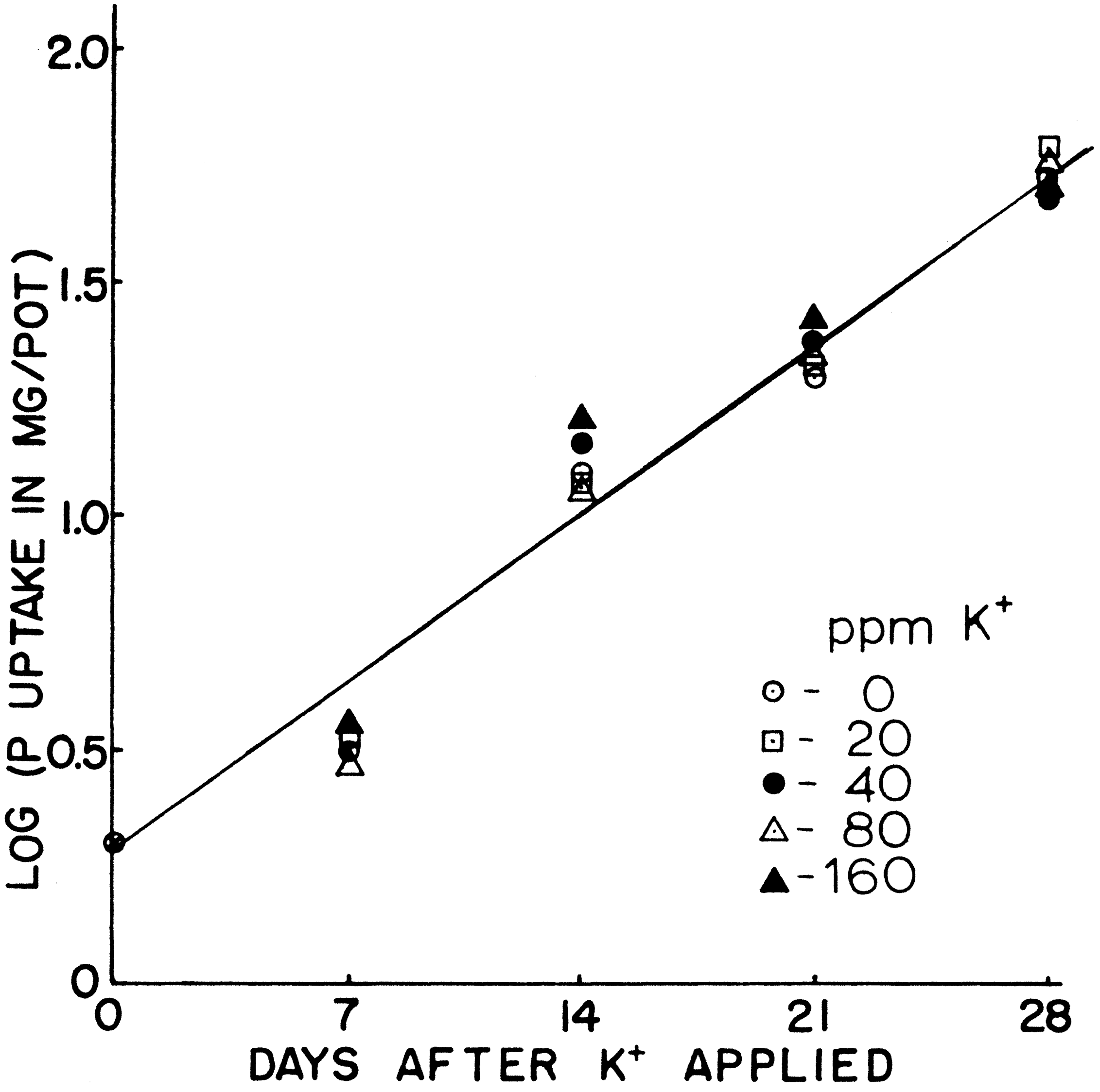

FIGURE 3. TOTAL PHOSPHORUS UPTAKE AT WEEKLY INTERVALS.

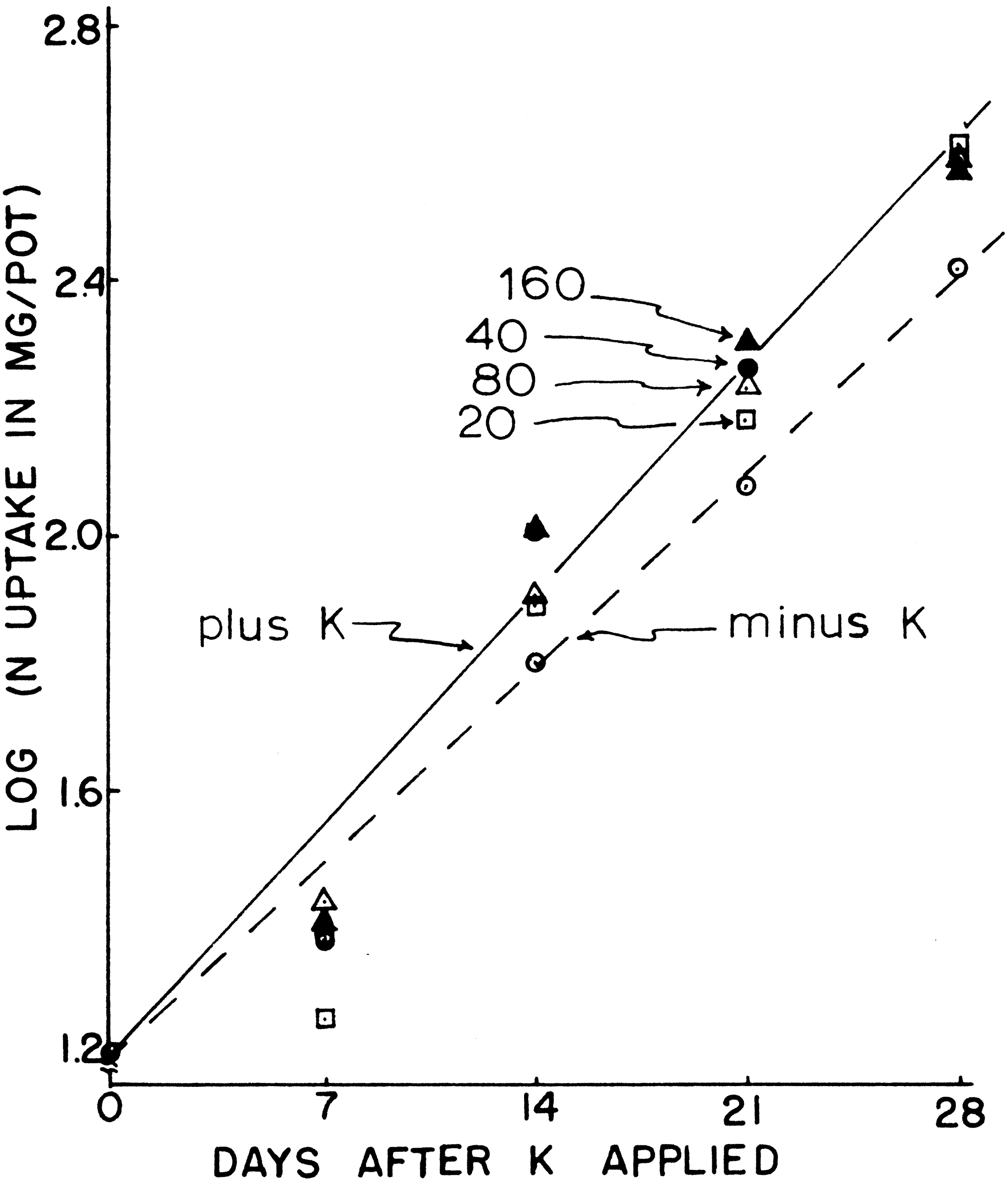

FIGURE 4. TOTAL N UPTAKE AT WEEKLY INTERVALS.

as a stimulating effect of potassium on nitrogen uptake. When the difference in the two slopes for nitrogen uptake are compared to those shown for the increase in total yield (Figure 1), it appears that the differences are similar. In general, a linear relationship existed between nitrogen uptake and yield, Figure 5.

Distribution of Cellular Phosphorus

The distribution of cellular phosphate for the initial (day-0) and three of the four weekly harvests is shown in Table 4. The plant tissue for the 21-day harvest was not dried completely after lyophilization, thus drying was completed in a forced-air oven. Subsequent biochemical analysis showed that oven drying altered the distribution of the cellular phosphate components. For this reason, the 21 day analyses were excluded.

A striking increase in trichloroacetic acid soluble phosphorus (TCA soluble-P) occurred with the minus K nutrient solution. The increase became evident for the 7-day harvest, especially when expressed as mg P/g (Hereafter this will be expressed simply as mg/g.). The accumulation of TCA soluble-P increased with time, both in actual concentration (mg/g) and as a percentage of the total cellular-P. For the 28-day harvest the minus K plant tissue was nearly 20% higher in TCA soluble-P than the average for the four K levels.

The TCA soluble-P fraction was separated into free

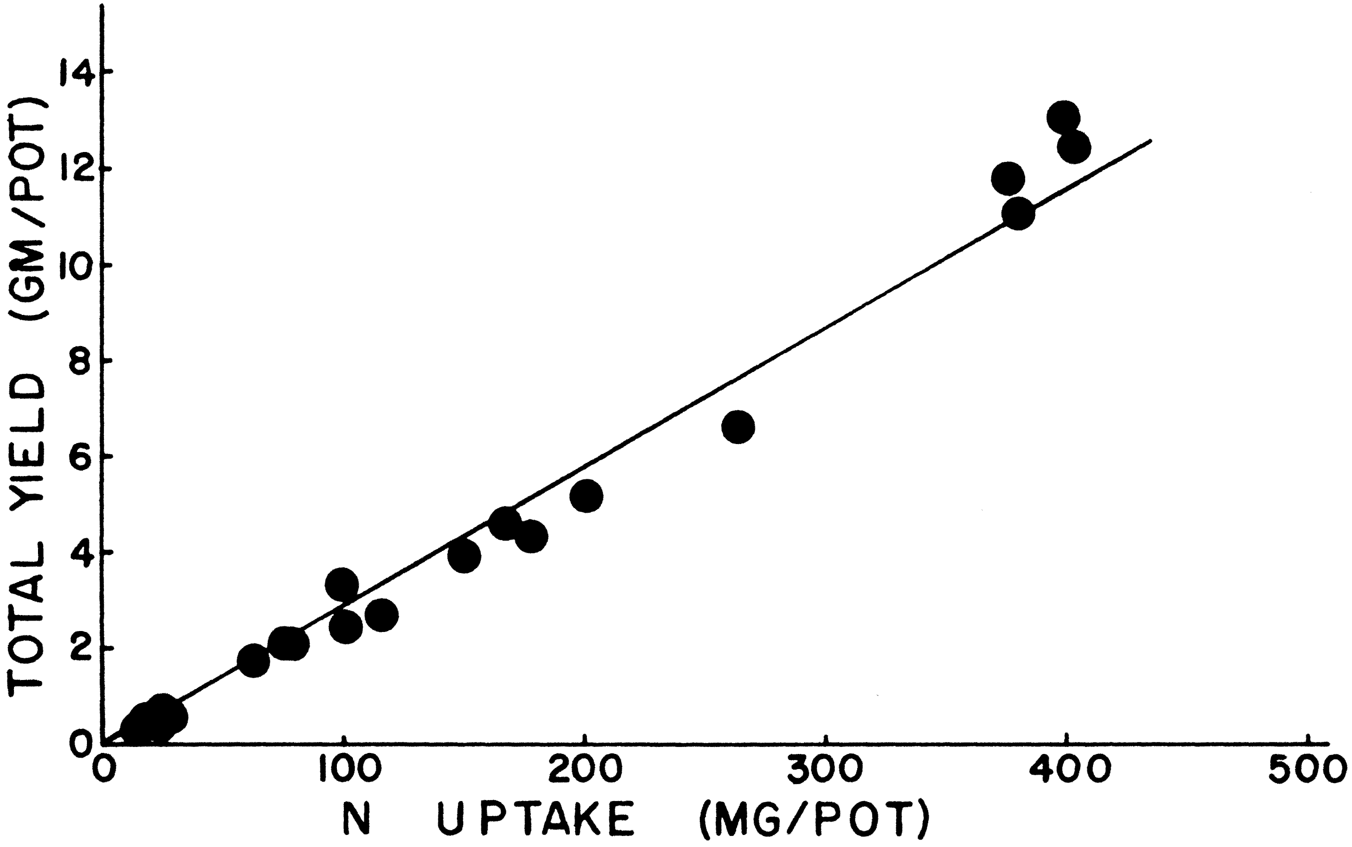

FIGURE 5. RELATIONSHIP OF N UPTAKE AND YIELD IN SOYBEANS.

Table 4. Effect of Time and Potassium Nutrition Levels on the Distribution of Cellular Phosphorus.

Harvest Date	K^+ Added	TCA Soluble-P						Lipid-P		Nucleic Acid-P	
		Total		Ortho-P		Organic-P					
Days after K added	ppm	mg/g*	%**	mg/g	%	mg/g	%	mg/g	%	mg/g	%
0	0	2.835	52.41	2.520	46.59	.098	1.81	0.898	16.60	1.791	33.11
7	0	3.780	62.58	3.612	59.80	.088	1.46	0.866	14.34	1.492	24.70
	20	3.543	62.35	3.563	62.71	.274	4.82	0.827	14.55	1.295	22.79
	40	3.512	60.58	3.228	55.68	.099	1.71	0.819	14.13	1.688	29.12
	80	3.268	63.85	2.913	56.92	----	-----	0.874	17.08	1.543	30.15
	160	3.449	61.00	3.258	57.62	.531	9.39	0.906	16.02	1.346	23.81
14	0	5.165	70.22	4.744	64.50	.669	12.49	0.866	11.77	1.457	19.81
	20	4.126	70.51	3.957	67.62	.546	9.33	0.906	15.48	1.386	23.68
	40	3.575	60.40	3.435	58.03	.330	5.57	0.866	14.63	1.295	21.88
	80	3.512	62.45	3.278	58.29	.315	5.60	0.906	16.11	1.366	24.29
	160	3.449	63.68	3.169	58.51	.325	6.00	0.890	16.43	1.252	23.12
28	0	6.260	79.85	4.764	60.77	.885	11.29	.748	9.54	1.254	15.99
	20	3.228	66.69	2.667	55.10	.581	12.00	.689	14.24	1.213	25.06
	40	2.480	57.27	2.195	50.69	.403	9.31	.689	15.91	1.219	23.15
	80	2.815	62.98	2.490	55.70	.423	9.46	.606	13.58	1.006	22.51
	160	2.303	53.31	2.067	47.85	.413	9.56	.689	15.95	1.151	26.64

* mg P/g of plant tissue

** % of total P

ortho-phosphate (inorganic phosphorus) and Norit-A nonadsorbed-P (organic-P)[3]. The organic-P fraction is composed primarily of sugar-phosphates.

Definite trends show an accumulation of both organic-P and Pi under low K nutrition. The trend for organic-P accumulation was evident at 14 days for minus K and at 28 days for the 20 ppm K level. Pi accumulation tends to occur somewhat later. The increase in organic-P may be related to the severity of visual potassium deficiency symptoms (Figure 2).

Lipid-P content was similar for tissue of a given age. However, when expressing the data as per cent of total cellular-P, there was a marked effect due to K. A 4 to 5% increase in lipid-P percentage was exhibited at 28 days, when comparing all K levels with minus K.

The nucleic acid-P (1N KOH extractable) decreased slightly in absolute concentration with increasing K levels; and it also decreased with time. However, the percentage of nucleic acid-P in plant tissue increased with added K. A 2 to 5% increase occurred at 14 days with added K; and at 28 days it increased to 6 to 12%.

Shifts in the distribution of cellular-P as influenced by K levels and age are shown in Figure 6. In general, a marked increase in TCA soluble-P and a concomitant decrease

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[3] Pi denotes ortho-phosphate to simplify the discussion.

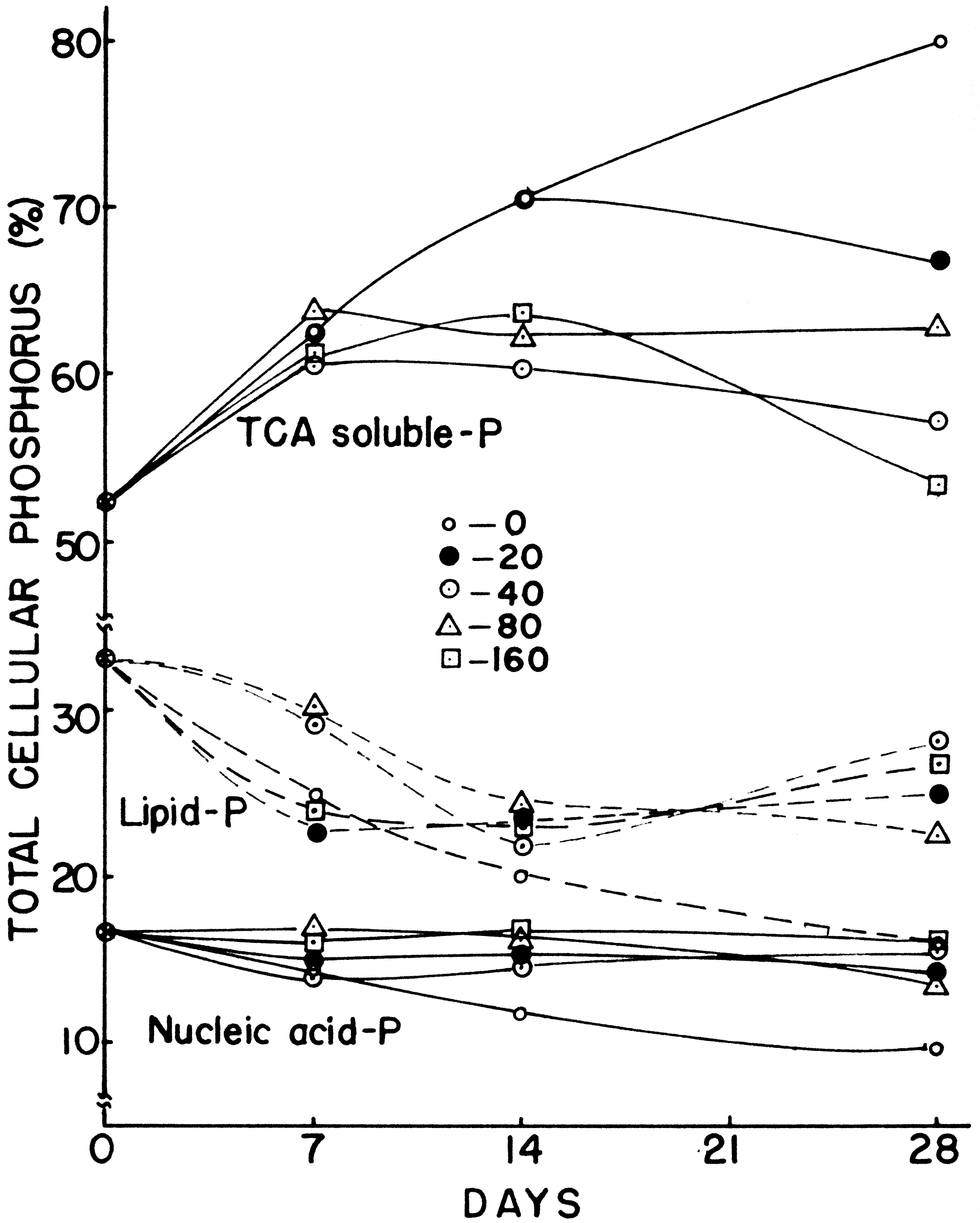

FIGURE 6. DISTRIBUTION OF GROSS CELLULAR PHOSPHORUS AS INFLUENCED BY POTASSIUM AND TIME.

in lipid-P and nucleic acid-P are exhibited for the minus K level. The extent of the increase and/or decrease in distribution became more distinct with advancing age or time.

Distribution of Cellular Nitrogen

The distribution of cellular nitrogen showed trends similar to those for the distribution of cellular-P, Table 5. In general, the trends were not evident until the 28-day harvest.

Both the total amount and percentage of TCA soluble-N increase markedly at 28 days with the minus K treatment. A slight increase in TCA soluble-N was observed at 14 days; but at 28 days the percentage had more than doubled, when comparing the four K levels with minus K.

The per cent nucleic acid-N increased slightly for all K levels at 28 days. However, the protein-N showed a very marked increase, 14 to 16% higher, with K treatments. The lipid-N distribution remained essentially constant.

Table 5. Effect of Time and Potassium Nutrition Levels on the Distribution of Cellular Nitrogen.

Harvest Date Days after K^+ added	K^+ Added ppm	TCA Soluble N mg/g*	TCA Soluble N %**	Lipid N mg/g	Lipid N %	Nucleic Acid N mg/g	Nucleic Acid N %	Protein N mg/g	Protein N %
0	0	9.244	21.60	4.341	10.14	18.885	44.12	10.33	24.14
7	0	4.984	12.13	3.023	7.35	7.288	17.73	25.81	62.80
	20	4.555	15.18	2.722	9.07	6.913	23.04	15.81	52.70
	40	3.974	9.81	3.612	8.92	13.400	33.08	19.51	48.17
	80	4.001	8.74	3.537	7.72	13.908	30.37	24.35	53.17
	160	4.555	11.85	2.219	5.78	10.782	28.08	20.84	54.27
14	0	6.056	16.51	3.473	9.26	6.806	18.15	21.16	56.43
	20	4.877	13.22	2.675	7.49	6.945	18.82	22.31	60.46
	40	5.681	13.49	3.130	7.43	6.774	16.09	26.52	62.99
	80	5.038	13.22	2.820	7.40	6.892	18.09	23.35	61.29
	160	4.984	15.06	2.497	7.54	6.838	20.66	18.78	56.74
28	0	13.692	34.14	3.057	7.62	9.423	23.50	13.93	34.74
	20	4.637	14.27	2.679	8.24	9.231	28.40	15.95	49.08
	40	4.627	13.41	2.887	8.37	9.175	26.59	17.81	51.62
	80	4.593	15.06	2.340	7.62	8.177	26.81	15.39	50.46
	160	4.308	13.38	3.019	9.38	8.369	25.99	16.50	51.24

* mg N/g of dry plant material

** % of total cellular N

EXPERIMENT II

After examining the data from Experiment I, it appeared desirable to study similar responses in phosphate and nitrogen metabolism with lower levels of potassium. Several revisions were also made in the greenhouse facilities to provide for automated irrigation. Plant populations were increased to provide adequate plant material for analyses to be conducted on each replication.

PROCEDURES

Physical and Culture Conditions

Culture system

The nutrient solutions were introduced into the plant container by the automated sub-irrigation technique described by Meyer and Anderson (1952). The plant containers were 2-gallon sized glazed crocks equipped with side drainage holes. Nutrient solutions were forced up through ¼-inch plastic tubing from 1-gallon black reservoirs into the plant containers by compressed air. The air pressure was regulated by an air-pressure reducer. The duration and frequency of irrigation was controlled by a solenoid valve-time clock combination. The plant containers were irrigated every two hours during the day and every four hours during the night. The same type of sand was used for this experiment as described in Experiment I.

Experimental design

Treatments were arranged in a split-plot design with harvest dates as the main plot and K levels as the sub-plots in each of two replications. Harvests were made at weekly intervals for three weeks.

The plant populations for this experiment were set at the following levels:

Harvest I: control, 100 plants harvested when treatments were initiated

Harvest II: 7 days-30 plants/pot

Harvest III: 14 days-20 plants/pot

Harvest IV: 21 days-10 plants/pot

Nutrient solution

The basic nutrient solutions were similar to those for Experiment I. The K levels ranged from 0 to 195 ppm K expressed in the form of millequivalents of K per liter of nutrient solution (meq K /l). Potassium was supplied as KCl at the following rates:

meq K^+/l	gms KCl/l	ppm equivalent
0	0	0
0.05	0.00373	1.95
0.10	0.00746	3.90
0.25	0.01865	9.75
0.50	0.03728	19.50
1.00	0.07455	39.00
5.00	0.37275	195.00

Establishment

The soybeans (Dorman variety) were seeded directly into the sand filled 2-gallon glazed crocks on October 9, 1963. The seedlings were thinned to the prescribed plant populations when ten days old. Five days later, October 24, 1963, the potassium treatments were applied. Morphologically, the seedlings were at the late seed-leaf or early first trifoliate leaf stage. A 16 hour photoperiod was used.

Biochemical Determinations

The harvesting procedure was similar to Experiment I; except that the plants were separated into stems and leaf plus meristematic tissue. The meristematic tissue was considered to be the area above the last trifoliate leaf petiole. These two separates were washed individually with the dilute solution of $CaCl_2$ (0.01%) as in Experiment I.

The subsequent biochemical determinations reported for this experiment pertain to the leaf plus meristematic tissue only. A 500 mg sample was used for extraction. The laboratory procedures were similar to those for Experiment I.

RESULTS

Dry Matter Production

There were marked differences in dry matter production per plant due to K levels and harvest dates, Table 6. The mean yield for all K levels was significantly higher for each successive week or harvest date.

Table 6. Dry Matter Production in Grams per Plant as Influenced by Potassium and Time.

K^+ applied	Harvest date (days)			
meq/1	7	14	21	Mean
0.00	.130	.246	.608	.328a*
0.05	.140	.280	.652	.357ab
0.10	.146	.322	.753	.407abc
0.25	.162	.343	.889	.464bc
0.50	.161	.352	.696	.403abc
1.00	.162	.318	.834	.438abc
5.00	.145	.370	1.044	.519c
Mean	.149	.319	.782	

*Values not having the same letter differ significantly at the 5% level.

The dry weight of the leaf tissue[4] increased logarithmically or exponentially with respect to time, Figure 7. Generally as the K level increased the rate (slope) of dry material accumulation also increased.

Chemical Composition and Nutrient Uptake

Potassium

The per cent potassium of the leaf tissue as affected by age and K level is shown in Table 7. The potassium percentage showed a highly significant response to added K and a significant response to harvest date.

The potassium levels x harvest date interaction was also highly significant. Partitioning of this interaction

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[4] "Leaf tissue" will be used to designate "leaf plus meristematic tissue".

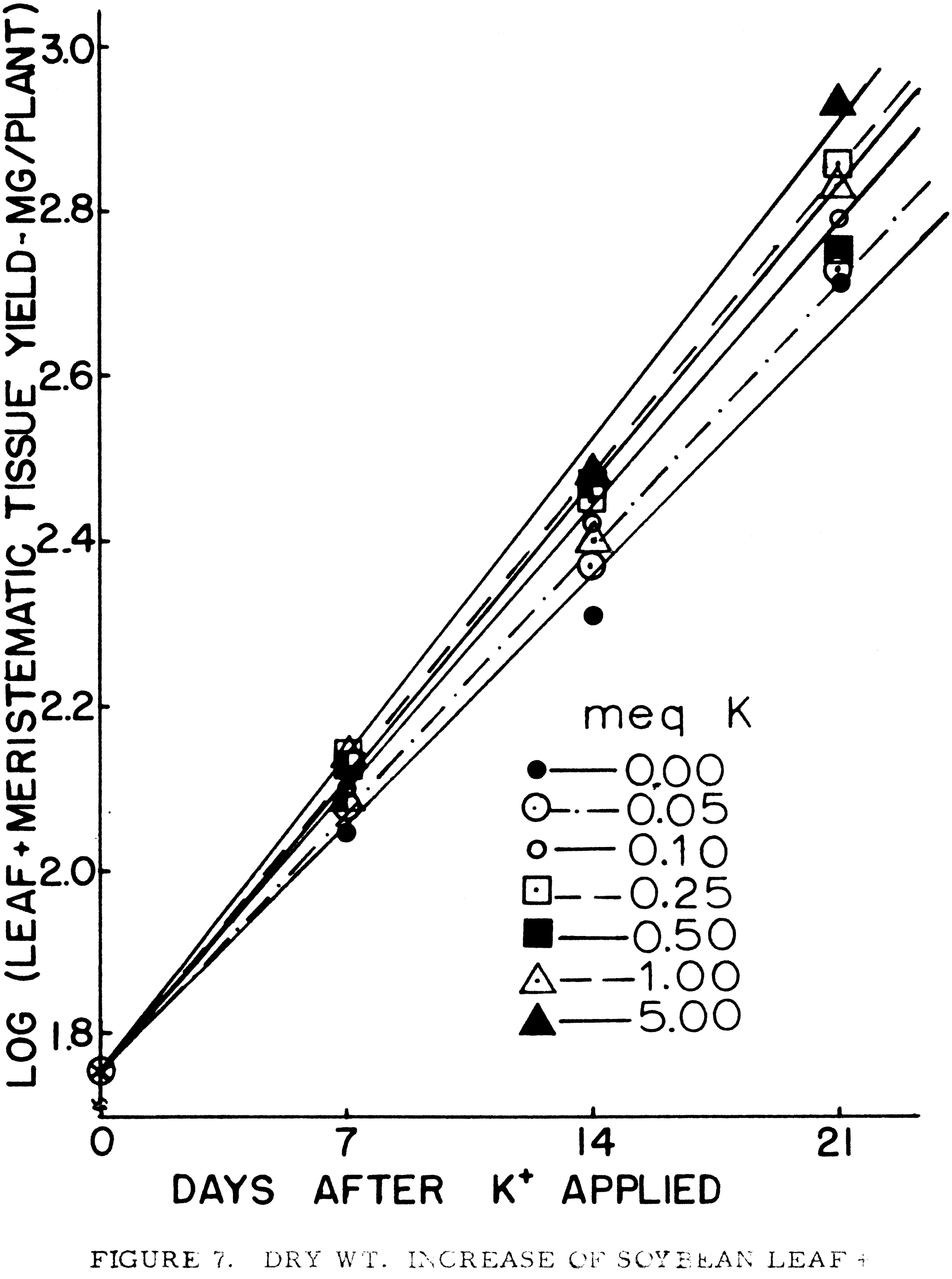

FIGURE 7. DRY WT. INCREASE OF SOYBEAN LEAF + MERISTEMATIC TISSUE AS INFLUENCED BY TIME AND K⁺ NUTRITION.

Table 7. Chemical Composition and Nutrient Uptake by Soybeans as Affected by Potassium Nutrition and Age.*

Harvest Date	K^+ Applied	Chemical Composition (%)			Nutrient Uptake in mg/plant		
Days	meq/1	K	P	N	K	P	N
0	0.00	2.50**	0.6262	5.94	1.425	0.036	3.39
7	0.00	1.73 d	0.7430	5.69	1.920	0.825	6.32
	0.05	1.89 cd	0.7316	5.59	2.268	0.878	6.71
	0.10	1.87 d	0.7165	5.60	2.356	0.903	7.06
	0.25	1.82 d	0.6848	5.33	2.530	0.952	7.41
	0.50	2.30 bc	0.6776	5.56	3.128	0.922	7.56
	1.00	2.48 b	0.6574	5.56	3.447	0.914	7.73
	5.00	3.97 a	0.6652	5.43	4.962	0.832	6.79
14	0.00	1.39 e	0.9876	5.47	2.850	2.025	11.21
	0.05	1.59 de	1.0352	5.57	3.721	2.539	13.03
	0.10	1.45 e	0.9376	5.79	3.814	2.466	15.23
	0.25	1.83 cd	1.0492	5.60	5.179	2.969	15.85
	0.50	2.09 c	0.8663	5.49	6.145	2.547	16.14
	1.00	2.62 b	0.9040	5.28	6.760	2.332	13.62
	5.00	3.95 a	0.7584	5.25	12.008	2.306	15.96
21	0.00	0.67 e	0.9602	5.29	3.390	4.859	26.77
	0.05	0.93 de	0.8884	5.03	4.948	4.726	26.76
	0.10	1.02 d	0.8851	5.29	6.263	5.434	32.48
	0.25	1.25 d	0.7927	5.31	9.000	5.707	38.23
	0.50	1.77 c	0.7784	5.09	9.965	4.382	28.66
	1.00	2.19 b	0.7911	4.96	14.804	5.248	33.53
	5.00	4.31 a	0.6930	5.14	36.807	5.918	43.90

* Average of two replications.

** Values within each date not having the same letter differ significantly at the 1% level.

(Appendix 2) showed a highly significant increase of potassium content with increasing levels of K within each harvest. In all cases the addition of 5.00 meq K/l gave a significantly higher per cent potassium. The leaf tissue from the remaining K levels varied with respect to potassium percentage from harvest to harvest. This may have been caused by a dilution of the endogenous K and applied K as yields increased with time.

Visual potassium deficiency symptoms were not observed until the last harvest. Mild, slight, and traces of potassium deficiency symptoms were noted for the 0.00, 0.05, and 0.10 meq of K/l, respectively. The per cent potassium in the leaf tissues for these K treatments was 0.67, 0.93, and 1.02%, respectively.

The uptake of potassium was highly associated with the amount of K added in the nutrient solutions.

Phosphorus

The per cent phosphorus generally decreased with increasing K levels; this trend is most evident at the 21-day harvest, Table 7. At this date the leaf tissue of the minus K treatment contained 0.96% phosphorus as compared to 0.69% phosphorus for the 5.00 meq K rate.

The differences in phosphorus uptake were small. A trend is indicated for a higher phosphorus uptake with increasing K at the 21-day harvest. This trend appears to be related to the yield increase, Table 6.

Nitrogen

Data on per cent nitrogen showed a significant effect due to harvest date, but not to K. The nitrogen percentage at the 21-day harvest was lower than at the 14 or 7-day harvest. There was no difference between the 7 and 14-day harvests. The decrease in per cent nitrogen with time was probably a dilution effect from the increased yield.

Nitrogen uptake as affected by K is shown in Figure 8. The rate of nitrogen uptake appears to be a linear logarithmetic function of time. The rate of nitrogen uptake increased with time, when K was added. A deviation from linearity is apparent for the 5.00 meq/l K level. This deviation was related to total yield increase rather than to K levels, Figure 9. Therefore, the increase in nitrogen uptake is a linear function of total yield rather than K level *per se*.

Extraction Time Study with 1*N* KOH

An extraction-time study was conducted on the lipid-free soybean leaf residue to determine the minimum time required to quantitatively extract the nucleic acids. With *Chlorella pyrenoidosa* cells, Baker and Schmidt (1963) reported that essentially all of the 1*N* KOH extractable phosphate was extracted in 30 minutes at 37° C. Herrmann (1964), working in the same laboratory, observed a similar trend for RNA-ribose and ultraviolet absorption at 260 mμ for a similar

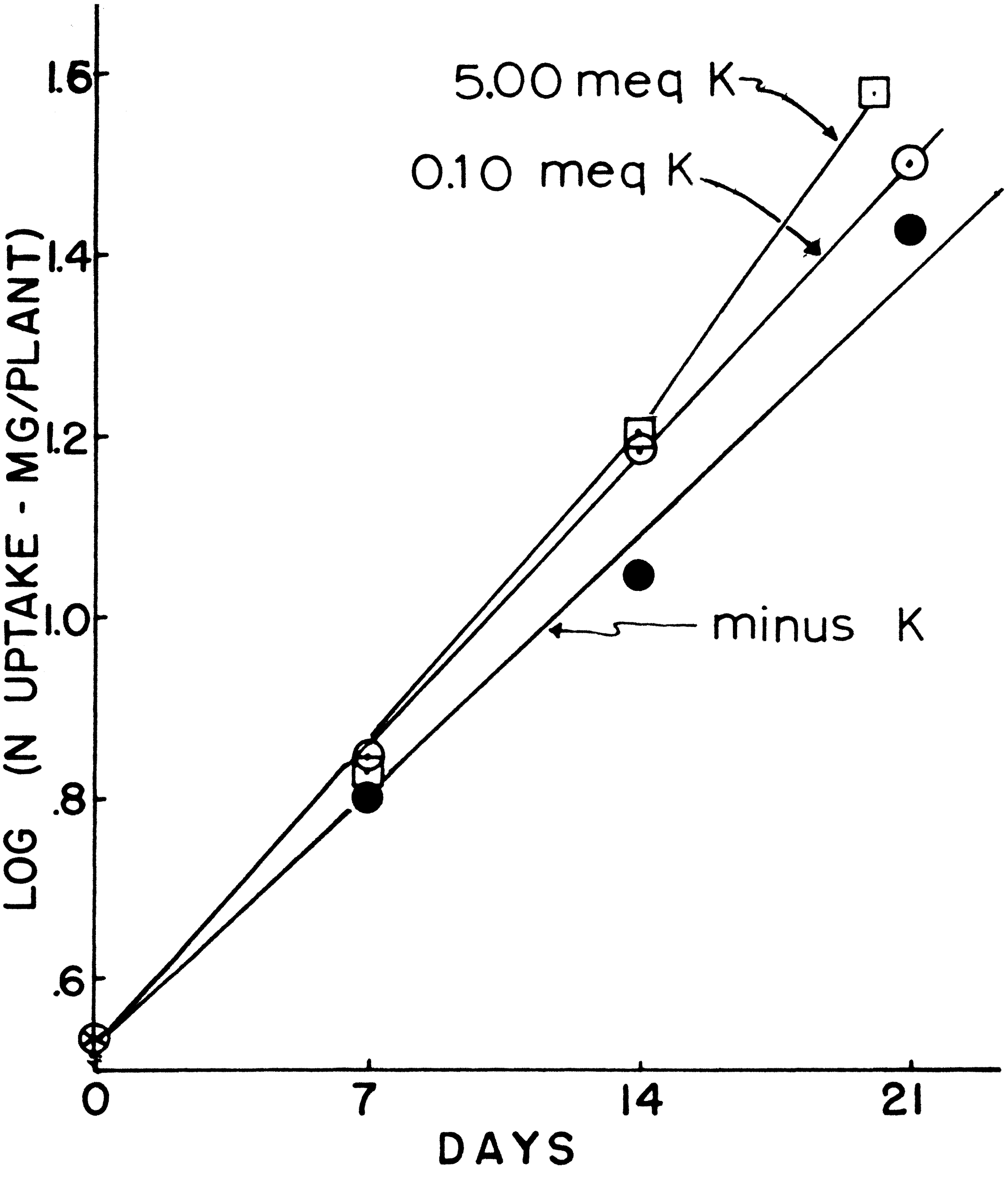

FIGURE 8. UPTAKE OF NITROGEN AS AFFECTED BY TIME AND POTASSIUM LEVELS.

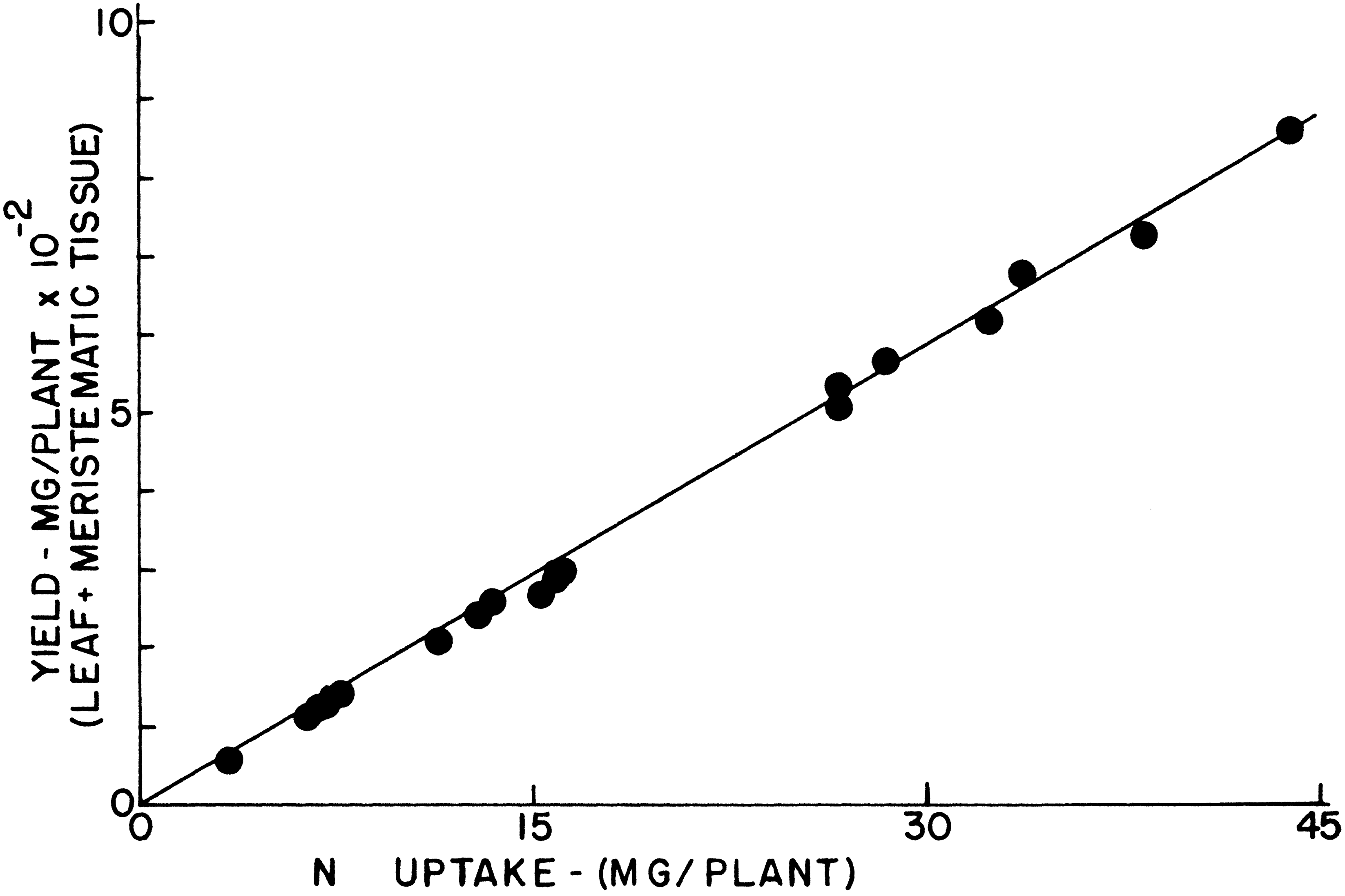

FIGURE 9. RELATIONSHIP OF NITROGEN UPTAKE AND YIELD.

extract.

The data of the continuous extraction of the lipid-free soybean leaf residue are shown in Figure 10. The total phosphorus extracted with 1N KOH increased up to 45 minutes. There was no further increase in total phosphorus extracted between 45 and 75 minutes. The slight increase in total phosphorus at 75 minutes and marked increase at 90 minutes indicates extraction of phosphoproteins.

Total nitrogen of the same extracts was determined. The extraction of total nitrogen increased up to 60 minutes, with no apparent increase between 60 and 75 minutes. After 75 minutes there was a gradual increase in total nitrogen. The increase after 75 minutes indicates that proteins were being hydrolyzed. It was concluded that the extraction of nucleic acids was completed at 60 minutes; hence the lipid-free leaf tissue residue was extracted for 60 minutes with 1N KOH at 37° C for nucleic acid analyses in the subsequent research.

Distribution of Cellular Phosphorus

The effects of varying K on the distribution of cellular phosphorus are shown in Table 8. The most marked effects occurred at the 21-day harvest, but the trends began to occur at the 7-day harvest. The mean values for all phosphate components combined for all dates for each K level, along with statistical significance are shown in Table 9.

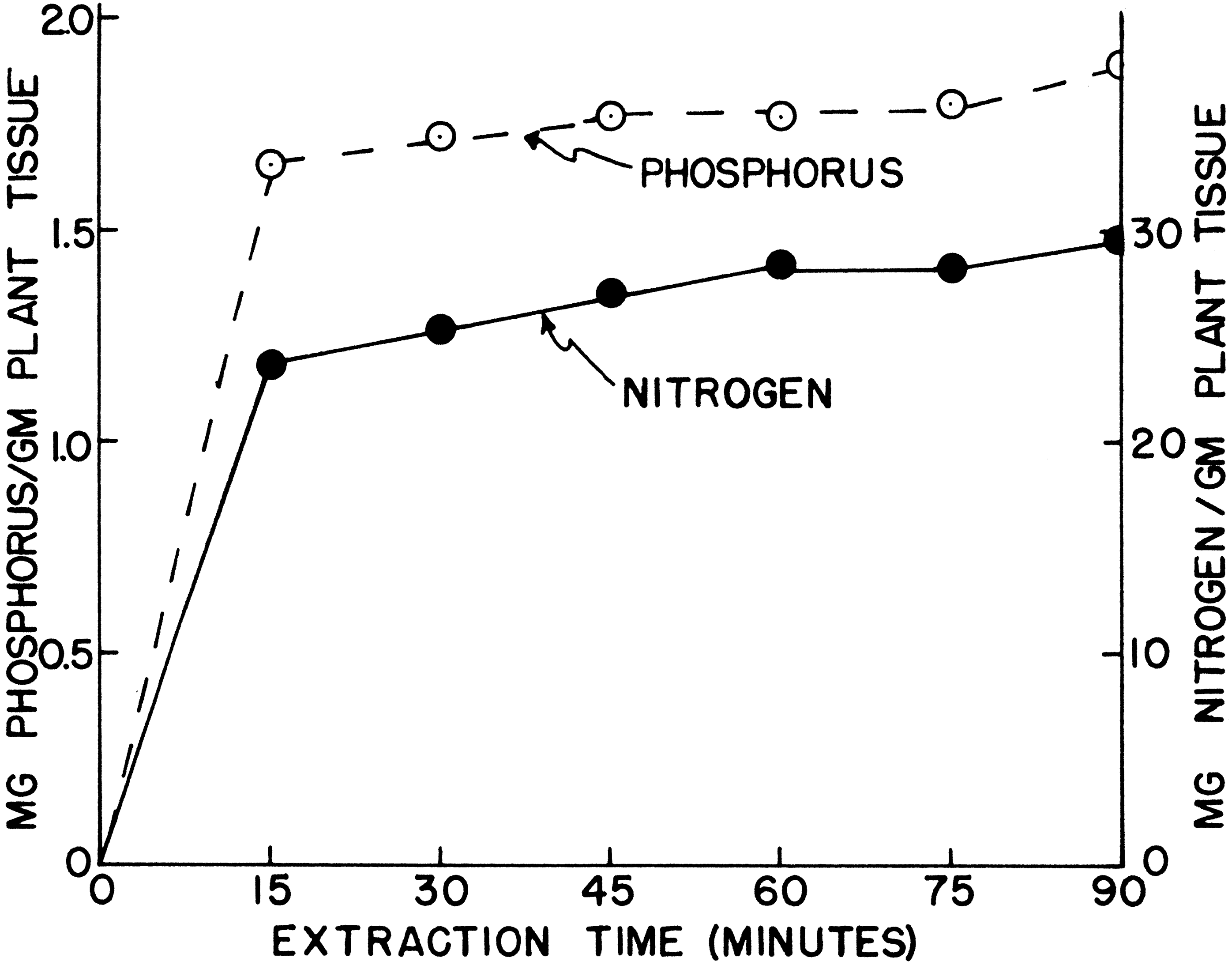

FIGURE 10. EXTRACTION OF NUCLEIC ACID PHOSPHORUS AND NITROGEN FROM THE LIPID-FREE SOYBEAN LEAF RESIDUE WITH 1 N KOH AT 37° C.

Table 8. Effect of Time and Potassium Nutrition on the Distribution of Cellular Phosphorus.*

Harvest Date	K$^+$ Applied	TCA Soluble-P									
		Total		Ortho-P		Organic-P		Lipid-P		Nucleic Acid-P	
Days	meq/l	mg/g**	%$^+$	mg/g	%	mg/g	%	mg/g	%	mg/g	%
0	0	3.468	55.38	3.367	53.77	0.081	1.29	0.745	11.90	1.394	22.26
7	0.00	4.350	58.70	3.948	53.12	.288	3.90	1.002	13.53	1.830	24.58
	0.05	3.962	54.64	3.450	45.23	.390	5.24	1.001	13.82	1.874	25.72
	0.10	3.688	51.46	3.258	45.48	.358	4.99	1.019	14.22	1.918	26.76
	0.25	3.806	55.63	3.566	52.17	.118	1.70	1.001	14.64	1.754	25.60
	0.50	3.623	53.44	3.462	51.06	.136	2.02	1.014	14.96	1.908	28.17
	1.00	3.652	55.55	3.338	50.76	.273	4.18	0.992	15.08	1.818	27.65
	5.00	3.563	53.56	3.267	49.18	.080	1.22	1.012	15.74	1.758	26.48
14	0.00	6.290	63.12	5.801	58.44	.460	4.36	0.948	9.72	1.776	18.16
	0.05	7.492	68.87	7.027	64.52	.374	3.46	1.004	9.34	1.844	17.10
	0.10	5.754	61.46	5.478	58.50	.195	2.10	0.981	10.47	1.910	20.40
	0.25	7.002	66.76	6.626	63.18	.170	1.60	0.988	9.42	1.982	18.89
	0.50	5.684	65.60	5.427	62.66	.088	1.03	1.003	11.58	1.851	21.38
	1.00	6.103	67.52	5.712	63.17	.344	3.83	0.969	10.72	1.818	20.11
	5.00	4.376	57.70	4.094	53.96	.133	1.76	0.987	13.02	1.706	22.48
21	0.00	6.186	64.50	5.604	58.44	.538	5.59	1.036	10.80	1.957	20.38
	0.05	5.205	58.66	4.773	53.78	.410	4.64	1.050	11.89	1.896	21.46
	0.10	4.972	56.48	4.758	53.96	.130	1.58	1.066	12.18	2.028	23.10
	0.25	4.358	54.94	4.156	52.44	.182	2.22	1.010	12.88	1.951	24.74
	0.50	4.437	56.48	4.060	52.12	.302	3.92	1.067	13.74	1.960	25.26
	1.00	4.278	54.06	4.018	50.78	.204	2.60	1.013	12.80	1.862	23.56
	5.00	3.780	54.55	3.668	52.93	.068	0.98	0.944	13.63	1.784	25.74

* Average of two replications

** mg P/g of plant material

$^+$ % of total cellular P

Table 9. Mean Value for Each Phosphate Component Combined for all Harvest Dates for Each K Level.

K^+	TCA Soluble-P						Lipid-P		Nucleic acid-P	
Applied	Total		Ortho-P		Organic-P					
meq/l	mg/g	%	mg/g	%	mg/g	%	mg/g	%	mg/g	%
0.00	5.609a*	62.10a**	5.118a*	56.72	.428a**	4.62	0.995	11.35e**	1.854	21.04c**
0.05	5.553ab	60.72a	5.083ab	54.51	.392a	4.45	1.018	11.68de	1.871	21.43bc
0.10	4.804bc	56.47b	4.498abc	52.65	.228ab	2.89	1.022	12.29cd	1.952	23.42abc
0.25	5.055abc	59.11ab	4.783abc	55.93	.156b	1.82	1.000	12.32cd	1.896	23.08abc
0.50	4.581cd	58.67ab	4.317cd	55.28	.175b	2.32	1.028	13.42ab	1.906	24.94a
1.00	4.677c	59.04ab	4.356bcd	54.90	.274ab	3.54	0.992	12.87bc	1.833	23.77ab
5.00	3.906d	55.27b	3.676d	52.02	.094b	1.32	0.981	13.96a	1.749	24.90a

* Values in the same column not having the same letter differ significantly at the 1% level.
** Values in the same column not having the same letter differ significantly at the 5% level.

Levels of Significance:

Total TCA Soluble-P
(1) mg/g: at 1%, potassium levels (K); at 5% harvest date (H); at 25%, K x H interaction
(2) % : at 1%, H; at 5% K; at 10%, K x H interaction

Ortho-P
(1) mg/g: at 1% K; at 5% H; at 10%, K x H interaction
(2) % : at 25% H and K; at 10%, K x H interaction

Organic-P
(1) mg/g: at 5%, K
(2) % : at 10%, K

Lipid-P
(1) mg/g: at 25%, K; < 25%, H and K x H interaction
(2) % : at 1%, K; at 5%, H; at 25%, K x H interaction

Nucleic acid-P
(1) mg/g: < 25%, H and K
(2) % : at 1%, K; at 10%, H

TCA Soluble-P

There was a marked increase in total TCA soluble-P with minus K as compared to the 5.00 meq K/l level, Table 9. The TCA soluble-P, expressed as either mg/g or per cent, was higher for the minus K than for the 5.00 meq K/l level.

Increasing K levels decreased the TCA soluble-P at a relatively uniform rate for each successive harvest. The TCA soluble-P content (both mg P/g and percentage) was highest at the 14-day harvest, intermediate at the 21-day harvest and lowest at the 7-day harvest.

Ortho-phosphate (Pi) showed a marked accumulation with decreased K levels, when expressed as mg/g. The 5.00, 1.00 and 0.50 meq K levels caused a marked decrease in Pi accumulation as compared to minus K. Potassium levels, harvest dates and their interaction did not effect Pi significantly, when expressed as a percentage of total cellular-P. Nevertheless, trends similar to those for mg P/g are observable.

As the amount of K increased, the mg/g of organic-P generally decreased. When expressed as percentage of total cellular-P, neither K levels, harvest date, nor their interaction was significant at the 5% level. However, increasing K levels caused the percentage of organic-P to decrease at the 10% level of significance.

Lipid-P

There were apparently no significant changes in the absolute amount (mg/g) of lipid-P due to K or harvest date. By expressing the data as percentages of total cellular-P, there were significant differences. Increasing K levels increased the per cent lipid-P, Table 8.

Lipid-P was highest at the 7-day harvest and lowest at the 14-day harvest. There was no difference in the per cent lipid-P between either the 7 and 21-day harvest or the 14 and 21-day harvest. Thus the per cent lipid-P increased during 0 to 7 days, decreased between 7 and 14 days, and then increased gradually between 14 and 21 days.

Nucleic acid-P

The percentage of nucleic acid-P was increased by added increments of K. At the 21-day harvest there was an increase in nucleic acid-P with each level of K. A slight deviation occurred with the 1.00 meq/l K level. Similar to the results found with lipid-P, the per cent nucleic acid-P decreased from the 7 to 14-day harvest. An increase in per cent nucleic acid-P was found from the 14-day to the 21-day harvest.

Distribution of Cellular Nitrogen

The distribution of cellular nitrogen as effected by harvest date, and K is shown in Table 10. The mean values for all nitrogen components combined for all dates for each K level, along with the statistical data are presented in Table 11.

Table 10. Effect of Time and Potassium Nutrition on the Distribution of Cellular Nitrogen.*

Harvest Date	K^+ Applied	TCA Soluble-N				Lipid-N		Nucleic Acid-N		Protein-N	
		Total		Norit-A Nonadsorbed							
Days	meq/l	mg/g**	%	mg/g	%	mg/g	%	mg/g	%	mg/g	%
0	0.00	17.617	29.66	8.654	14.57	3.046	5.13	22.243	37.45	16.494	27.77
7	0.00	11.534	20.32	9.774	17.20	9.382	16.46	25.334	44.46	10.649	18.76
	0.05	10.614	19.21	9.018	16.37	8.676	15.50	25.050	44.55	11.560	20.74
	0.10	9.010	16.09	6.801	12.14	8.972	16.03	26.918	47.96	11.099	19.91
	0.25	8.861	16.58	6.940	13.01	8.806	16.56	25.798	48.86	9.835	18.50
	0.50	9.272	16.69	7.814	14.08	8.303	14.96	26.032	46.84	11.944	21.52
	1.00	8.694	15.58	7.220	12.92	7.972	14.54	26.446	47.60	12.538	22.53
	5.00	7.245	13.34	6.055	11.09	7.068	14.00	24.561	45.30	14.926	27.36
14	0.00	7.453	13.62	6.596	12.06	7.378	13.48	24.906	45.54	14.962	27.35
	0.05	7.441	13.36	6.547	11.76	7.836	14.06	24.435	43.88	15.988	28.70
	0.10	6.778	11.76	5.831	10.11	7.458	12.91	26.410	45.76	17.044	29.57
	0.25	6.830	12.20	5.522	9.86	8.832	15.78	25.960	46.35	14.378	25.66
	0.50	5.626	10.24	4.648	8.47	8.648	15.76	27.221	49.59	13.406	24.40
	1.00	5.114	9.70	3.926	7.44	7.927	15.02	25.674	48.62	14.084	26.66
	5.00	4.528	8.62	3.250	6.19	8.593	16.36	24.528	46.72	14.851	28.30
21	0.00	11.940	22.60	7.331	13.86	6.114	12.22	24.098	45.52	10.399	19.64
	0.05	8.230	16.30	4.668	9.28	6.912	13.80	25.866	51.46	9.292	18.45
	0.10	7.954	15.06	5.198	9.82	7.110	13.42	26.426	49.94	11.409	21.58
	0.25	6.802	12.88	4.060	7.66	7.618	14.31	26.334	49.52	12.346	23.30
	0.50	5.958	11.71	3.382	6.64	7.101	13.95	27.710	54.44	10.131	19.91
	1.00	5.446	11.02	3.261	6.52	7.279	14.61	28.020	56.18	8.855	18.19
	5.00	5.350	10.40	3.108	6.04	4.932	9.60	25.870	50.33	15.248	29.66

* Average of two replications

** mg N/g of dry plant tissue

% of total N

Table 11. Mean Value for Each Nitrogen Component Combined for all Harvest Dates for Each K Level.

K^+ Applied	TCA Soluble-N				Lipid-N		Nucleic Acid-N		Protein-N	
	Total		Norit-A nonadsorbed							
meq/l	mg/g	%	mg/g	%	mg/g	%	mg/g	%	mg/g	%
0.00	10.309a*	18.85a*	7.901a	14.37a	7.741	14.06	24.780	45.17d	12.004b**	21.92b**
0.05	8.762b	16.29b	6.742b	12.47ab	7.808	14.46	25.117	46.63cd	12.280b	22.63b
0.10	7.918bc	14.30bc	5.943bc	10.69bc	7.847	14.12	26.585	47.69bc	13.184ab	23.69b
0.25	7.498bcd	13.89bc	5.507c	10.18c	8.419	15.55	26.031	48.07bc	12.186b	22.49b
0.50	6.952cde	12.88cd	5.282c	9.73cd	8.017	14.89	26.988	50.29ab	11.827b	21.94b
1.00	6.418de	12.10cd	4.802cd	8.96cd	7.726	14.73	26.713	50.80a	11.826b	22.46b
5.00	5.708e	10.79d	4.138d	7.78d	7.031	13.32	24.986	47.44cd	15.008a	28.44a

*Values in the same column not having the same letter differ significantly at the 1% level.
**Values in the same column not having the same letter differ significantly at the 5% level.

Levels of Significance

Total TCA Soluble-N
(1) mg/g: at 1%, potassium levels (K), at 25%, harvest date (H) and K x H interaction
(2) % : at 1%, K; at 25%, H; <25%, K x H interaction

Norit-A Nonadsorbed-N
(1) mg/g: at 1%, K; at 25%, H; <25%, K x H interaction
(2) % : at 1%, K; at 25%, H; <25%, K x H interaction

Lipid-N
(1) mg/g: at 25%, H
(2) % : <25%, H, and K x harvest date interaction

Nucleic acid-N
(1) mg/g: at 25%, K
(2) % : at 1%, K; at 25%, K x H interaction

Protein-N
(1) mg/g: at 5%, K; at 10%, H; at 25%, K x H interaction
(2) % : at 5%, K; at 25%, H; <25%, K x H interaction

TCA soluble-N

The accumulation of TCA soluble-N (mg/g and per cent) was inversely related to K levels. The TCA soluble-N did not differ with harvest date or with the K level x harvest date interaction. Thus, the decreases in total TCA soluble-N with added levels of K were consistent for each harvest date. Similar effects were noted for the Norit-A nonadsorbed-N.

Lipid-N

Lipid-N as mg/g or per cent of total cellular-N, was not effected by K or harvest date.

It appears that there was a decrease in lipid-N with increasing K at the 21 and 7-day harvests. However, this trend was reversed at the 14-day harvest.

If the lipid-N fraction can be taken as an indication of chlorophyll content, then K may indirectly regulate chlorophyll synthesis causing a general increase in lipid-N at the 14-day harvest. The marked decrease in lipid-N for the 5.00 meq/l K level at the 21-day harvest may be a dilution effect due to the rapid dry weight accumulation. In addition, a marked increase in protein-N occurred concurrently with the decreased lipid-N for the 5.00 meq K treatment. This would be additional evidence of the dilution effect suggested for the decrease in lipid-N at the 21-day harvest.

Nucleic acid-N

When the nucleic acid-N was expressed as mg/g there was no statistical significance due to treatments. However, there appears to be a slight increase in nucleic acid-N for the intermediate K levels.

The same data when expressed as percentages of total-N, showed a very striking increase in nucleic acid-N with applied K. With 0.50 and 1.00 meq/l K rates there was a higher nucleic acid-N percentage than for 0.00, 0.05, and 5.00 meq/l K rates. The per cent nucleic acid-N increased with each increment of K up to the 5.00 meq/l rate. There was no significant difference among the 0.00, 0.05 and 5.00 meq/l K levels.

Protein-N

Statistical analysis showed that there were some significant effects of K levels on protein-N. The highest K level (5.00 meq) resulted in more protein-N, with no significant differences among the remaining K levels. At the 21-day harvest there was a 10% increase in per cent protein-N between the minus K and 5.00 meq/l K level. This difference amounted to approximately 5 mg/g of protein-N. There was no marked effect due to either harvest date or K level x harvest date interaction.

DISCUSSION

Dry matter accumulation was increased logarithmically or exponentially with time, regardless of applied K levels. This was found for both total herbage (Experiment I) and leaf tissue (Experiment II). The primary effect of added K in the nutrient solutions was to accelerate the rate (slope) of dry matter accumulation with time. The rate of logarithmetic dry matter accumulation progressively increased with time for each increment of K in Experiment II.

The K level needed to prevent deficiency symptoms increased with time, in Experiment I. As much as 40 ppm of K was not sufficient to prevent slight potassium deficiencies at the 28-day harvest. The data indicate that endogenous K from seeds was sufficient for "normal" growth up to the 7-day harvest or a total of 32 days after planting (25 days establishment plus 7 days after K treatments).

The percentage of phosphorus in the plant tissue was inversely related to the amount of K supplied. This agrees with the work of Kroontje (1956). These data could lead to the erroneous conclusion that K retards the uptake of phosphorus. However, further calculations showed that total phosphorus uptake was not affected by applied K. The uptake of phosphorus was similar for all K levels at a given harvest date, but increased progressively with time. Phosphorus uptake was a linear logarithmetic function of time regardless of K level. Thus, the increased per cent phosphorus was due to the concentrating effect caused by the lower yields as K levels decreased. From these data it appears that phosphorus uptake is a "passive" reaction, relatively independent of growth. Nitrogen uptake was a linear logarithmetic function of time. It appears that increasing K levels stimulated nitrogen uptake, Figures 4 and 8. However, this was found to be an indirect effect of K caused by its direct effect on increasing the yield. A direct linear relationship was found between nitrogen uptake and total yield, Figures 5 and 9.

Baker and Schmidt (1964) reported considerable hydrolysis of lipid-P with increased storage time of the unextracted *Chlorella pyrenoidosa* cells. The decrease in lipid-P was associated with a quantitative increase in TCA soluble-P. They attributed the increase in TCA soluble-P to increases in ortho-phosphate and Norit-A nonadsorbed-P. To obtain a quantitative estimation of nucleotide-P (Norit-A adsorbed-P), the cold TCA extract must be passed through the Norit-A column immediately after extraction (Schmidt, 1964). Without this precaution, the di- and tri-P nucleotides may be rapidly hydrolyzed to the nucleotide mono-P with a concomitant increase in ortho-phosphate (Pi).

The soybean seedling material used in this study was stored for one to two months before extraction, in most cases. Due to limited laboratory space and equipment, it was impossible to subject the cold TCA extract to Norit-A adsorption columns immediately after extraction. For the reasons mentioned above, the percentage of Pi found in the TCA soluble fraction is somewhat magnified.

With the analytical methods used, a direct quantitative estimation of the di- and tri-P nucleotides was not possible; therefore, an indirect estimation was calculated. Assuming that the concentration of non-nucleotide Norit-A adsorbed-N and P compounds was constant, by determining the Norit-A adsorbed P:N ratio an indirect estimate of the di-P plus tri-P nucleotides was calculated, Table 12. Increases in adsorbed P:N ratios indicate that proportionately more P than N was adsorbed. Thus, indirect evidence of an increase in the poly-P nucleotides can be obtained.

A marked increase in the adsorbed P:N ratio was found, especially when comparing the two extreme K levels. A 2.88, 3.96 and 2.72-fold increase in the adsorbed P:N ratio for the 7, 14, and 21-day harvest, respectively, was noted. This indirect evidence indicates that potassium functions either directly or indirectly in the phosphorylating mechanism of the adenlyic acid system (AMP, ADP and ATP). This is in agreement with the work of Pressman and Lardy (1955) for coupled oxidative phosphorylation. A similar function of potassium may be operative in photosynthetic phosphorylation. Thus, low levels of potassium may inhibit the formation of energy-rich

Table 12. Distribution of Norit-A Adsorbed Compounds as Influenced by Time and Potassium*.

Harvest date	K^+ Applied	Norit-A adsorbed-P		Norit-A adsorbed-N		Adsorbed P/N ratio	
Days	meq/l	mg P/g**	% Total-P	mg N/g**	% Total-N	mg/g	%
0	0.00	.020	0.32	8.963	15.09	.0022	0.212
7	0.00	.114	1.53	1.760	3.14	.0648	0.487
	0.05	.122	1.71	1.602	2.84	.0762	0.602
	0.10	.072	0.99	2.208	3.96	.0326	0.250
	0.25	.123	1.75	1.922	3.57	.0640	0.490
	0.50	.024	0.34	1.457	2.62	.0165	0.130
	1.00	.040	0.61	1.474	2.72	.0271	0.224
	5.00	.216	3.16	1.190	2.25	.1815	1.404
14	0.00	.030	0.32	0.856	1.56	.0350	0.205
	0.05	.090	0.90	0.894	1.66	.1007	0.542
	0.10	.081	0.86	0.958	1.65	.0846	0.521
	0.25	.206	1.99	1.308	2.34	.1575	0.850
	0.50	.170	1.91	0.977	1.77	.1740	1.079
	1.00	.047	0.52	1.188	2.26	.0396	0.230
	5.00	.149	1.98	1.278	2.44	.1166	0.811
21	0.00	.045	0.47	4.608	8.75	.0098	0.054
	0.05	.021	0.23	3.562	7.02	.0059	0.033
	0.10	.084	0.93	2.782	5.24	.0302	0.177
	0.25	.020	0.28	2.742	5.21	.0073	0.054
	0.50	.075	0.95	2.576	5.06	.0291	0.188
	1.00	.055	0.70	2.185	4.49	.0252	0.156
	5.00	.044	0.63	2.242	4.30	.0196	0.147

* Average of two replications

** mg/g of dry plant tissues

phosphate bonds due to the reduced ATP or poly-P nucleotide levels.

If a mechanism(s) is present to establish a priority or dominance of certain metabolic process, such as respiration, for chemical energy (ATP); then a potassium stress could cause an increase in respiration with respect to the other processes. With this assumption, a striking increase in TCA soluble compounds or intermediates would be expected. When nitrogen is applied as reduced-N (NH_3 or NH_4^+) a specific metabolic pathway is present to reduce the deleterious effect of the excess reduced-N. This is accomplished by the formation of amide compounds (primarily glutamine and asparagine). This reaction also requires ATP (Webster, 1959), thus causing a further drain on the ATP pool. An increase in soluble-N, especially asparagine under low K fertilization has been reported by Griffith et al. (1960) and several others.

If the first metabolic "priority" role of potassium is related to general-P metabolism rather than general-N metabolism, then changes in the distribution of cellular-P should occur at lower K levels than those indicated for the distribution of cellular-N. A comparison of Figures 11 and 12 shows that this occurred.

Marked changes in P-distribution were found for the 0.05, 0.10 and 0.25 meq K/l levels. The redistribution of cellular-P generally levels off at the 0.25 meq K/l rate. The

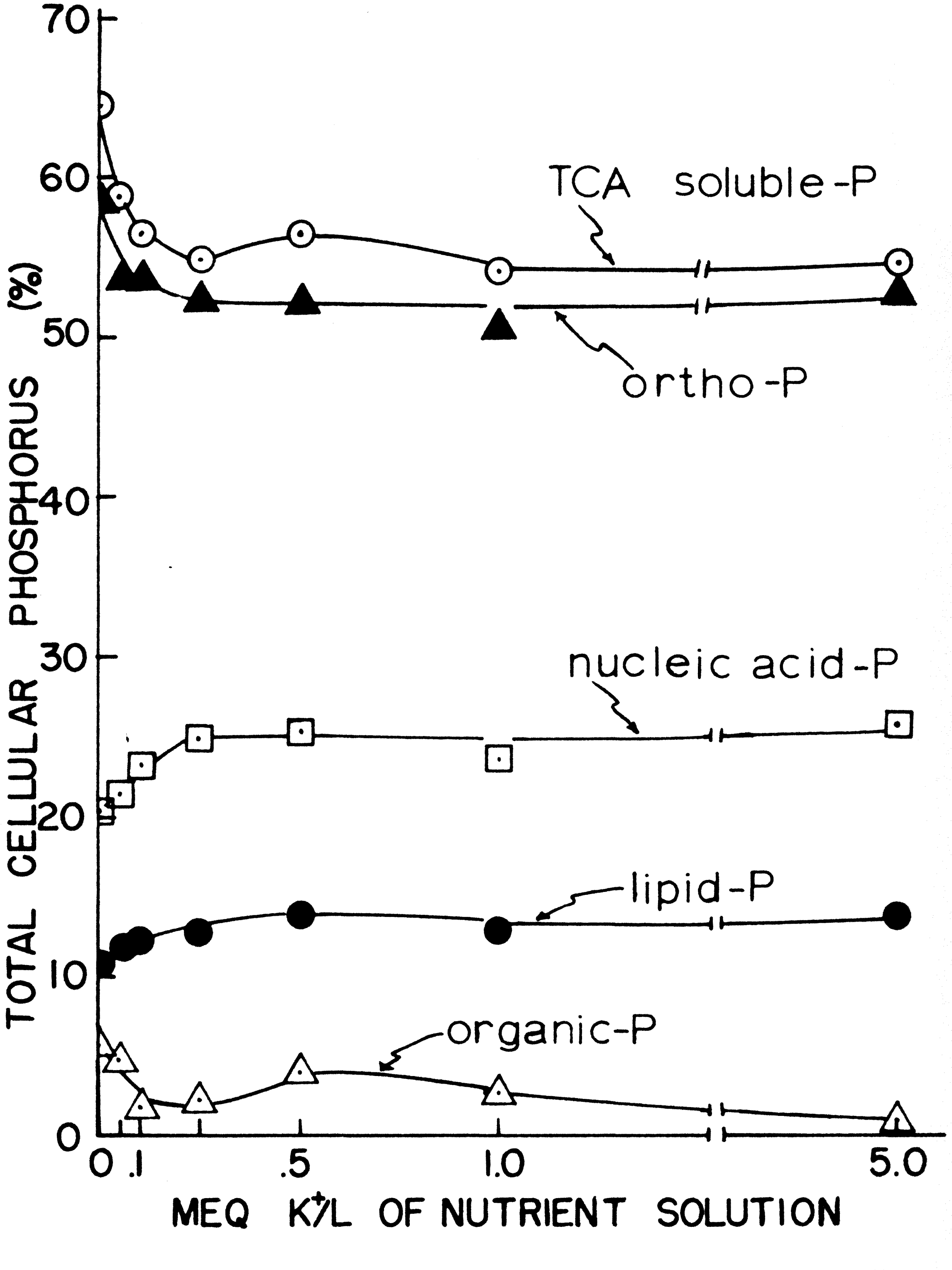

FIGURE 11. DISTRIBUTION OF CELLULAR PHOSPHORUS 21 DAYS AFTER APPLYING POTASSIUM.

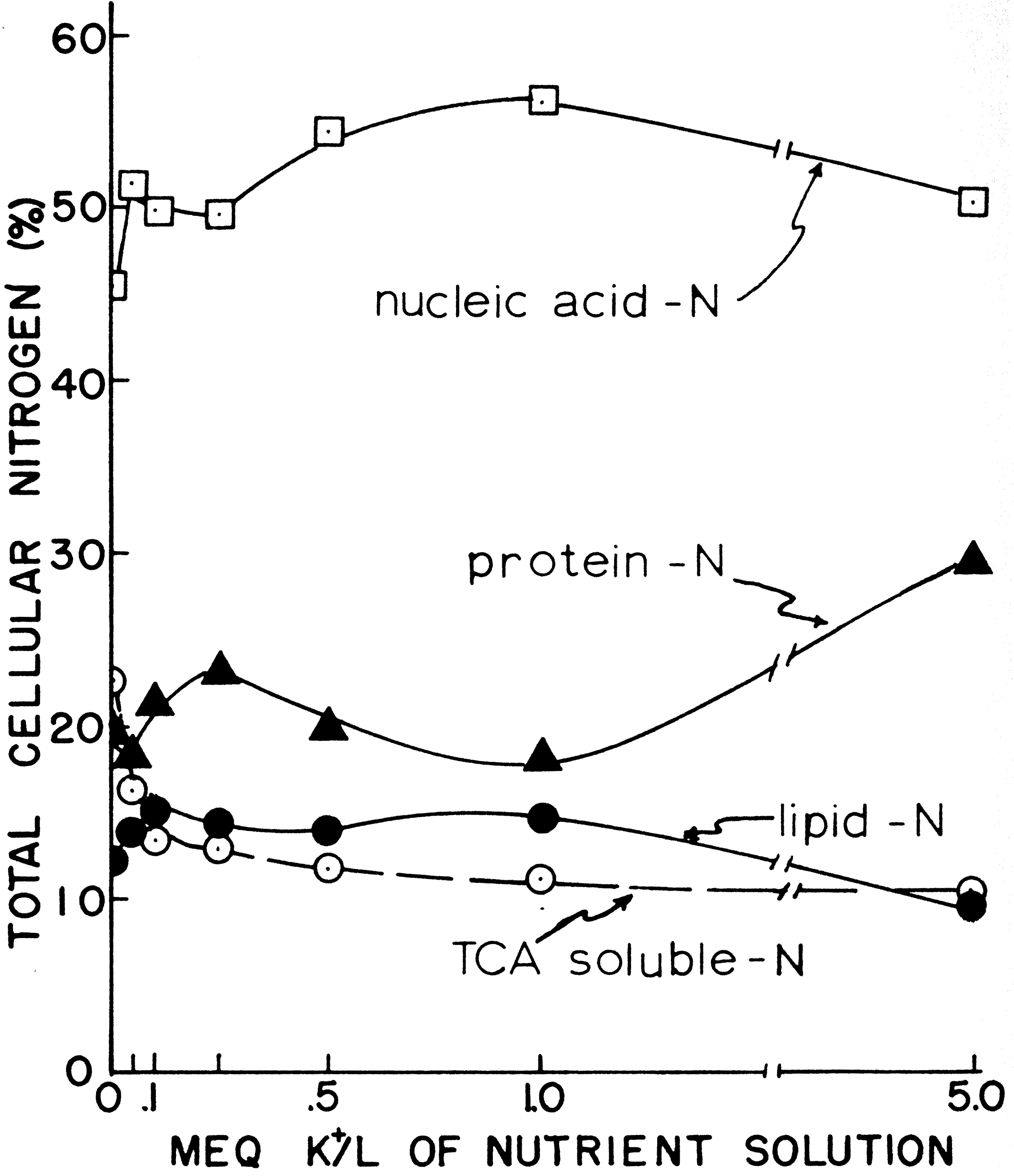

FIGURE 12. DISTRIBUTION OF CELLULAR NITROGEN 21 DAYS AFTER APPLYING POTASSIUM.

redistribution of TCA soluble-N and nucleic acid-N did not stabilize until the 1.00 meq K level.

The marked increase in nucleic acid-N at the 0.05 meq level may be a reflection of the "specific" potassium requirement for nucleic acid base synthesis reported by Okuda and Nakamigawa (1958). The initial increase in protein-N at the 0.25 meq level may be an indication of the potassium requirement for peptide-protein synthesis reported by Webster (1959). The decreased protein-N at the 0.50 and 1.00 meq levels is probably a reflection of a nucleic acid "stress".

The decrease in lipid-N at the 5.00 meq level is probably caused by the dilution effect of increased yield and increased cellular protein.

The observation that K is somewhat irreversibly retained in the mitochondria (Gamble, 1962) and the requirement of K in coupled oxidative phosphorylation in mitochondria (Pressman and Lardy, 1955), leads to the conclusion that K in some way regulates general phosphorus metabolism. If this is true, then the role of K in such diverse pathways as carbohydrate metabolism, protein synthesis, photosynthesis, respiration, etc. is explainable. Since high energy phosphate bonds are required for each of these pathways, and if K regulates phosphorus metabolism (and/or intermediate interconversions); then K indirectly influences essentially all other metabolic processes.

The highly speculative aspects of this discussion are acknowledged. However, the hypothesis that K regulates the level or concentration of poly-P nucleotides can be determined experimentally in the laboratory.

The following studies are suggested to test the validity of this hypothesis: (1) more accurate determinations of poly-P nucleotides as influenced by applied K levels using the precautions previously discussed, and (2) the incorporation of inorganic P into the various organic fractions as influenced by K levels, utilizing radio-active P^{32}.

SUMMARY AND CONCLUSIONS

Two experiments were conducted in the greenhouse to study the influence of potassium on phosphorus and nitrogen metabolism in soybean seedlings. The sand culture technique for growing the plants was used. The herbage was fractionated into acid soluble, ethanol-ether soluble (lipid compounds) and 1N KOH soluble (nucleic acids) components. Nitrogen and phosphorus analyses were made on each of the fractions.

The increase in yield was essentially a linear logarithmetic (exponential) function of time. Increased levels of K in nutrient solutions increased the rate (slope) of the logarithmetic dry matter accumulation, depending on the amount of K added. The uptake of K increased with each increment of K.

The K level required to prevent visual potassium deficiency symptoms increased with plant age. Endogenous K from seeds appeared to be sufficient to support near "normal" growth for at least 32 days after planting. A minimum potassium content of approximately 1.60% prevented visual potassium deficiency symptoms. When the potassium percentage exceeded 2.20%, luxury consumption was indicated.

Potassium levels did not effect phosphorus uptake. The percentage of phosphorus was inversely related to K levels. This was explained by a dilution effect caused by the increased yield with increasing K. Nitrogen uptake was apparently stimulated by K. However, this was an indirect effect caused by higher yields with increasing K. There was a direct linear relationship between nitrogen uptake and yield.

An extraction-time study on the lipid-free soybean leaf residue with 1N KOH was made. Essentially all extractable phosphorus and nitrogen was removed within 45 minutes and 60 minutes, respectively. Extraction for more than 75 minutes hydrolyzed proteins, causing a gradual increase in extractable phosphorus and nitrogen.

Norit-A adsorbed P:N ratios were used to indirectly estimate the relative changes in poly-nucleotide-P (ATP + ADP) with increasing K levels. It was found that the calculated P:N ratio increased with increased K. This is indirect evidence that potassium may function in the formation of high-energy phosphate bonds. The inverse relationship found between potassium levels and ortho-phosphate accumulation is additional evidence that potassium functions in the esterification of inorganic phosphate. There is a strong implication that a metabolic role of potassium may be associated with coupled oxidative phosphorylation. A similar potassium function may be operative in photosynthetic phosphorylation.

The results agree with the work of Webster (1959) that potassium has a direct function in peptide-protein synthesis.

Under an energy stress, a defense mechanism that establishes a priority or dominance of one metabolic process over another was postulated. It was concluded that phosphorus metabolism exhibited a priority over nitrogen metabolism under a general potassium stress.

Based on these results and the work of others, it was concluded that potassium functions in the following metabolic processes: (1) peptide-protein synthesis, (2) nucleic acid base synthesis, (3) esterification of inorganic phosphate, and (4) enzymatic catalyst or activator.

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APPENDIX

Appendix 1. Analysis of Variance of Dry Matter Yield in Grams per Plant (Experiment I).

Source	df	SS	MS	F
Total	59	35.845774		
Reps	2	0.197645	0.098822	5.31*
Harvest date	3	31.851578	10.617193	570.97**
Error (a)	6	0.111569	0.018595	
K-levels	4	1.114032	0.278508	13.98**
K x H	12	1.933325	0.161110	8.08**
K within H_7	4	0.000375	0.000094	---
K within H_{14}	4	0.055122	0.013780	---
K within H_{21}	4	0.19367	0.027342	1.37
K within H_{28}	4	2.882493	0.720623	36.16**
Error (b)	32	0.637625	0.019926	

Appendix 2. Analysis of Variance of Percent Potassium (Experiment II).

Source	df	SS	MS	F
Total	41	38.9882		
Reps	1	0.1660	0.1660	8.60
Harvest date	2	2.2474	1.1237	58.22*
Error (a)	2	0.0386	0.0193	
K-levels	6	34.4711	5.7452	234.50**
K x H	12	1.6233	0.1353	5.52**
K within H_7	6	7.4679	1.2446	50.80**
K within H_{14}	6	9.8914	1.6486	67.29**
K within H_{21}	6	18.7351	3.1225	127.45**
Error (b)	18	0.4418	0.0245	

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ABSTRACT

Phosphorus and Nitrogen Metabolism in Soybeans as Influenced by Potassium

by

Paul R. Henderlong

The effect of K on P and N metabolism in soybean seedlings, *Glycine max*, Var. Dorman, was studied in two greenhouse experiments. Yield, nutrient uptake, and changes in the distribution of cellular P and N compounds served as criteria for evaluating K effects. The yield increased exponentially with time regardless of K treatments; however, increasing K levels increased the rate of yield accumulation.

Phosphorus uptake was not associated with K levels. An increase in N uptake was associated with increased dry matter production rather than K levels, *per se*. An inverse relationship was found between per cent P and K levels. This was attributed to a dilution effect due to the increased yield with increasing K levels.

An extraction-time study on the lipid-free soybean leaf residue with 1*N* KOH, showed that essentially all of the extractable P and N was extracted within 45 and 60 minutes, respectively. Longer extraction times caused gradual protein hydrolysis.

Norit-A adsorbed P:N ratios were used to indirectly estimate the relative changes in poly-nucleotide-P (ATP and

ADP) associated with K levels and ortho-P accumulation; indicating that K functions either directly or indirectly in the esterification of inorganic-P in coupled oxidative phosphorylation. From the data presented, it was concluded that under a general K stress, P metabolism exhibited a priority over N metabolism for K.

Based on these data, K was found to function in the following metabolic processes: (1) peptide-protein synthesis, (2) nucleic acid base synthesis, and (3) esterification of inorganic-P.