EFFECT OF TEMPERATURE ON UPTAKE AND UPWARD TRANSLOCATION OF PHOSPHORUS IN WHEAT

A Thesis

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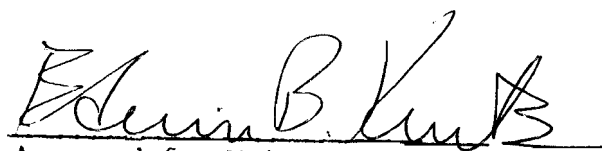

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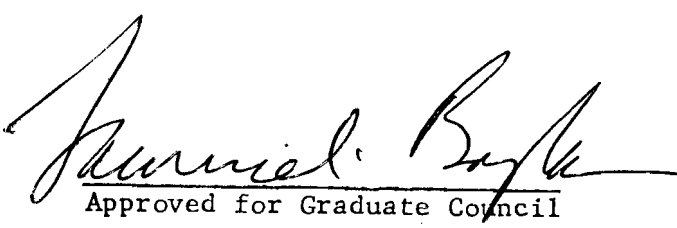

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INTRODUCTION

In his search for food, clothing and shelter, man is constantly changing his natural surroundings to suit his needs. He is ever introducing plants and animals in areas where nature did not intend them to be. For instance, oat is a cool climate plant, but with intelligent manipulation man is able to grow it in a warmer climate than its natural ecological habitat. The trick, man has learned, is to understand the limits of a biological system and then find ways of overcoming the limits. As Kurtz (5) stated for desert agriculture,

> "A knowledge of how desert plants tolerate high temperatures, and the use of this information for the chemical cure of climatic ills of economic plants, will help to solve the critical food problem of the world by permitting agriculture to extend into new lands and increasing yields of presently cultivated areas."

But climatic ills are not the only limiting conditions. Wheat, a cool season plant is cultivated in Kenya where average temperatures range between 10^{o}C and 30^{o}C throughout the year. However, one of the limiting growth factors for this plant in its new habitat is the nutrient element phosphorus. This element is not readily available in the volcanic soils of Kenya. Response to phosphate fertilizers is usually high for most crop plants; Russell (13) reports a recovery of 67 per cent

of elephant grass (Pennisteum purpureum) when superphosphate fertilizers are applied. To plan for a comprehensive fertilization program for such crop plants growing in an exotic environment, therefore, more knowledge is needed to understand how the plants absorb and translocate the element phosphorus.

A lack of phosphorus in plants will lead to serious problems, since it may prevent other nutrients from being acquired, and may prevent synthesis of some plant metabolites. The significance of this mineral as a nutrient element is shown by its participation in a variety of metabolic schemes as photosynthesis, glycolysis, synthesis of starch, fats, proteins and nucleic acids. This element is needed at various points in the plant where any one of these processes is occurring. Biddulph (1) has suggested that a "pool" of phosphorus in a usable form is maintained throughout the plant in a relatively uniform concentration.

Like many mineral nutrients of soil origin, phosphorus is absorbed into a plant through the root system. Millar et al (7) states that the actual absorption of nutrient minerals, of which phosphorus is one, is both passive and active. It is passive when the nutrient ion diffuses into the "outer" space of the root cell, and becomes an active process when energy is

required to transport the ion from the "outer" space into an "inner" space across a semi-permeable membrane. Most of the uptake, however, occurs near the tip of newly formed roots or root hairs and the process requires the energy released by respiration.

Over a long period of time mineral absorption in plants may be influenced by the stage of growth. An older plant may be expected to absorb more of a nutrient element than a younger plant because the older plant has increased absorptive surfaces and increased total metabolism. But, this concept does not seem to fit the absorption pattern of phosphorus. Roger and Link (11), in comparing uptake of P^{32} with K^{42} in alfalfa and oat roots, reported that four-day-old plants absorbed more phosphorus than fifteen-day-old plants. Russell (13) stated that a young plant will take up nearly all its phosphate from a band of soluble fertilizer suitably placed with respect to the seed. In addition to the stage of growth, the length of exposure to the nutrient element will determine the amount a plant will absorb. Lewis and Quirk (6), studying phosphate movement into young wheat roots, found that the root accumulated noticeable amounts of phosphorus after the tenth day of experimentation.

Another factor that will influence mineral uptake in plants is temperature. Temperature has a profound influence on the

absorption of mineral salts. In general, an increase in temperature is expected to speed up the absorption rate, and a decrease to lower it. Devlin (3) stated that increased temperature accelerates salt absorption up to a certain maximum; beyond that maximum point, any further increase in temperature will inhibit salt absorption and eventually terminate the process. Working with potassium, Sutcliffe (14), found that washed carrot slices absorb more potassium at 40°C than at any other temperature. As the temperature increases beyond 40° mark, absorption declines sharply. Rudgers, et al. (12) reported that phosphorus concentrations in corn roots decline at 30°C-20°C day-night, as compared to 20°C-10°C day-night temperatures under growth chamber conditions.

There is ample evidence showing that the upward movement of salts accumulated in the roots is through the xylem ducts. It has been demonstrated in different ways that besides functioning as a transpiration stream, xylem vessels are the only known means of translocating salts to aerial parts of plants. Tolbert and Wiebe (15) have shown that inorganic phosphorus is a major form of phosphorus being transported through xylem ducts of barley plants.

It is well known that an increase in temperature will increase transpiration, if the stomates are open. It would be expected, therefore, that salt uptake should simultaneously increase with increased transpiration. But, Paulsen and Rotimi (9) observed that stems of soybeans grown under growth chamber

conditions at 30°C-20°C day-night sequence contained lower concentrations of phosphorus than those at 20°C-10°C day-night temperatures. At similar growth chamber temperatures, Rudgers, et al. (12) reported a decline in phosphorus concentration in corn leaves at higher temperatures. This shows that an increase in temperature decreases phosphorus uptake in the plants studied.

The increased temperature affects physiological processes in plants. Petinov and Razmaev (10) working with wheat and corn plants reported that temperatures of 40°C and 42°C respectively lowered respiration rates. Molotkovskii (8), studying the effect of high temperature on adenosinetriphosphate (ATP) activity in a squash plant observed that enzyme activity dropped at 50°C, with a concurrent increase in the amount of inorganic phosphorus.

A review of the literature cited above, has shown the influence temperature has on absorption and transport of mineral salts in plants. Although nutrition experiments have used wheat plants, the author could not locate any report dealing with the influence of temperature on mineral uptake and translocation in wheat. The purpose of the present study was to investigate the effect of temperature on uptake and upward translocation of phosphorus in wheat plants at three stages of growth. The study will give an indication as to how wheat, an exotic plant to Kenya, may respond to phosphorus fertilization at the various temperature regimes found in that country.

MATERIALS AND METHODS

The experiment was designed to test three sets of plants germinated and grown in a growth chamber at three day-night temperature regimes: 21°C-15°C; 27°C-21°C; and 32°C-27°C. Each set of plants was divided into three groups to provide growth stages as follows: 2 weeks, 4 weeks, and 6 weeks. All stages were to receive equal amounts of radioactive phosphorus at their respective temperature regimes.

The experiment was begun when seeds of Parker wheat (Triticum tritici L), a spring wheat variety obtained from a local seed company, were treated against seed-borne diseases. They were seed-dressed by putting them in a 5% Clorox solution for five minutes. One hundred seeds were selected at random and planted in petri dishes, and the dishes placed in the growth chamber. For the first group of plants the growth chamber (Percival, Model PT 80, No. 8336.2) was set to a 21°C day and 15°C night sequence with an illumination intensity of 1200 f.c. 800 cm above the crocks on a 12-12 hour day-night cycle. Three days later, after the seeds had germinated, seedlings were transplanted into inert sand contained in 1.4 liter crocks. The crocks were numbered from 1 to 12 inclusive, with 8 seedlings planted to each crock. The seedlings received Hoagland's complete nutrient solution (Hoagland and Arnon, 4) supplied from 2-liter

plastic containers. Attached to each nutrient container was a flexible plastic tube through which the nutrient flowed by gravity into a hole at the bottom of each crock of wheat plants.

The nutrient level in each container was held relatively constant by adding more nutrient solution to the containers for the first three days. After three days, when the seedlings were firmly rooted, the nutrient level was gradually lowered to give the developing roots room to ramify into the substrate.

One week after transplanting, all seedlings were thinned, reducing them from 8 to 5 seedlings per crock. Three days later, a second thinning was undertaken in four of the crocks, reducing the seedlings from 5 to 3 per crock. The second thinning was necessary in order to allow room for the application of radioactive phosphorus.

It was hoped that the radioactive phosphorus would be received before or on the day the seedlings reached two week stage, but it was received a week late. Therefore, the first application of radioactive phosphorus, at two weeks old, was omitted.

The first application of radioactive phosphorus was on the four week old plants, which missed radioactive phosphorus at the two week stage. Before applying radioactive phosphorus, the nutrient supply from plastic containers to the four crocks was cut off and the holes at the bottom of each crock sealed. Radioactive phosphorus (P^{32}) supplied by Amersham/Searle as

orthophosphate was diluted in Hoagland's solution and added directly to the sand in the crocks. Each crock received 0.25 millicuries of the radioactive phosphorus and the four crocks were replaced in the growth chamber.

The plants were allowed to absorb and translocate the radioactive phosphorus for a variety of periods. The periods were 30 minutes, 60 minutes, 90 minutes, and 120 minutes, respectively. After each time period, the three plants from each crock were removed, their roots rinsed in running water, and 2-3 cm sections harvested from certain parts of the plants. The sections were cut from tips of older open leaves, young folded leaves, and the base of the stem, 3 cm above the sand culture. The various sections were labeled and dried in a vacuum desiccator at room temperature.

Drying of the plant material took about 5 days. The sections then were weighed and put on labeled metal planchets, each planchet with a diameter of 3 cm and 2 mm deep. The amount of radioactivity in the various plant tissues was determined by using an automatic Geiger-Muller gas flow counter (Nuclear-Chicago, Planchet Sample Changer, Model 1042, and Decade Scaler, Series 8703), which was set to record counts per minute. Background counts were taken at the time of counting. All counts, sample and background counts were replicated three times, and mean counts obtained for each sample and background.

The activity of P^{32} was corrected for decay.

Three days before the second application of P^{32}, the seedlings in the next four crocks were again thinned from 5 seedlings to 3 seedlings. At the 6 week stage after transplanting, P^{32} was fed to this group of plants exactly in the same way as the first group (at the 4 week stage). Radiation counts were also determined for these samples by the same procedure as for the former samples.

A two-day interval was required to clean the growth chamber and set it at a higher temperature regime of $27^{o}C$-$21^{o}C$ for the second set of plants. With the exception of the temperature regime, the conditions in the growth chamber and handling procedures from planting up to and including radiation counting were repeated for the second set of plants at the $27^{o}C$-$21^{o}C$ temperature regime, and for the third and last set of plants grown at the highest temperature regime of $32^{o}C$-$27^{o}C$. Radioactive phosphorus was applied to all the three stages of growth (2, 4, and 6 weeks) designed for each set of plants. No stage was omitted in the last two sets of plants.

Radioactivity of P^{32} was corrected for decay from the day of counting back to the day of the experiment. Half life of P^{32} is 14.3 days (Chase and Rabinowitz, 2). The counts for the four time periods (30, 60, 90, and 120 minutes) were added and divided by 4 to obtain a mean at 75 minutes.

RESULTS

General

The results from Tables I, II, III, IV, show translocation rates of P^{32} at various temperature regimes and growth stages. Since the present work did not aim at studying translocation rates, the tables have been included to show the observations and how mean values for Table IV and Figure 1 were obtained.

Specific activity of the sampled parts of plants showed definite variations in concentration of P^{32} at the different temperature regimes and at the three different stages of growth (Table IV). In general, the stem portions had the highest activity at all three temperature regimes and at all different stages of growth. Young folded leaves had the next highest specific activity, and the tips of older leaves had the lowest activity.

The results (Table IV and Figure 1) from all the treatments show higher specific activity in plants at a lower temperature regime than the ones at a higher temperature. The lowest activity was obtained from plants at the highest temperature regime. At a younger stage of growth, there was more activity than at an older one. Having briefly outlined the pattern portrayed by the specific activities obtained, let us now look at the results of each set of plants individually.

Plants at 21-15°C temperature regime

(a) Two-week old plants

As mentioned earlier, the 2-week stage of growth at this temperature was skipped due to a delay in obtaining radioactive phosphorus.

(b) Four-week old plants

Activity of P^{32} (Table I) was quite high in the stem compared with the young and old leaves. The ratio of activity in the stem to that in the leaves is large, indicating more concentration of P^{32} in the stem portion of the plant. Morphologically, the stem is closer to the source of mineral nutrients than leaves, and it has large conducting vessels. Probably that is why it has more activity. The possibility of contamination with nutrient solution containing P^{32} should not be discounted, however.

(c) Six-week old plants

Stem portions of the 6-week old plants like the 4-week old plants, had more activity than both the young and old leaves. But on the whole, the activity of P^{32} was lower in the 6-week old plants as compared with 4-week old (Table I). Nevertheless, both stages of growth conform to a common pattern of uptake; that is, the highest concentration of P^{32} is in the stems, lower in the young leaves, and lowest in the older leaves. Figure 1 shows clearly this pattern of uptake, at this

TABLE I. Activity of P^{32} in wheat plants at 4 and 6 weeks of growth at 21-15°C day-night temperatures. The activities are the means of triplicate samples and are counts per minute per milligram dry tissue.

Stage of Growth	Time in minutes after application of P^{32}	OBSERVED COUNTS/MINUTE			Interval between application and counting	COUNTS/MINUTE CORRECTED FOR DECAY		
		Stems	Young leaves	Old leaves		Stems	Young leaves	Old leaves
4 weeks	30	3133	318	142	17 days	7175	727	326
	60	3289	601	245		7531	1377	562
	90	2336	451	168		5349	1034	385
	120	5032	338	210		11523	773	481
6 weeks	30	243	48	25	19 days	614	120	64
	60	464	338	101		1173	854	256
	90	622	180	141		1555	455	356
	120	999	353	371		2528	892	938

temperature regime.

Plants at 27^{o}-21^{o}C temperature regime

(a) Two-week old plants

Table II and Figure 1 show the results obtained from the set of plants that grew at a temperature regime of 27^{o}-21^{o}C, day-night cycle. Once again stems had high specific activity, compared with both young and old leaves. One remarkable observation is that, though the activity of P^{32} in stems was high the ratio between the stem and leaf activities is small.

(b) Four-week old plants

Four-week old plants at this temperature did not accumulate as much P^{32} as the same age of plants at 21^{o}-15^{o}C temperature regime. Those at a higher temperature had lower activities, but there was less variation than the same age of plants at a lower temperature. However, stem activity still stood up high, but again the ratio between stem and leaves is very much narrowed. The older leaves had a higher specific activity (deviating from the pattern set in other groups of plants, already discussed). Probably this was just a normal variation among the leaves.

(c) Six-week old plants

Apparently, older plants absorb less P^{32}. Results from Figure 1 show that the activity of P^{32} in the sampled portions were markedly reduced. However, the stem portions as usual had

the highest activity. But when compared with same age of plants at a lower temperature regime, the activity in 6-week old plants at this temperature regime was very much reduced.

Plants at 32°-21°C temperature regime

(a) Two-week old plants

Table III and Figure 1 show that P^{32} concentration was quite low at this temperature compared with the same age of plants at a temperature regime of 27°-21°C, but the results conform to a common pattern of uptake. The stems had the highest specific activity, and the young and old leaves had essentially the same activity.

(b) Four-week old plants

As mentioned above, the older the plants got the less P^{32} they took up. Here again (Table IV and Figure 1) show that activity from the 4-week old plants was less than the 2-week old. Once again, the 4-week old plants at this temperature had less specific activity than same age of plants at lower temperatures.

(c) Six-week old plants

The last stage of plants to be tested at the highest temperature was the 6-week old plants. The results obtained (Table IV and Figure 1) from this age of plants indicates that they did not take up much of P^{32}. This stage had very low specific activities, especially in the leaves (both young and old). Like the same age of plants at the 27°-21°C temperature regime, the leaves had the lowest concentrations of P^{32}.

However, the stem portions in this group of plants had slightly higher counts than the stems of the same age of plants at 27-21°C degree regime, thus deviating from the usual pattern.

TABLE II. Activity of P^{32} in wheat plants at 2, 4 and 6 weeks of growth at 27-21°C day-night temperatures. The activities are the means of triplicate samples and are counts per minute per milligram dry tissue.

Stage of Growth	Time in minutes after application of P^{32}	OBSERVED COUNTS/MINUTE			Interval between application and counting	COUNTS/MINUTE CORRECTED FOR DECAY		
		Stems	Young leaves	Old leaves		Stems	Young leaves	Old leaves
2 weeks	30	147	96	28	58 days	2508	1647	476
	60	222	146	52		3798	2506	896
	90	438	151	56		7501	2576	956
	120	622	147	78		10643	2514	1327
4 weeks	30	170	79	71	18 days	409	191	171
	60	410	314	299		988	756	719
	90	441	365	297		1062	881	716
	120	714	554	599		1722	1336	11443
6 weeks	30	184	51	60	4 days	224	62	73
	60	349	97	79		426	118	96
	90	333	96	104		406	117	127
	120	666	120	105		813	146	128

TABLE III. Activity of P^{32} in wheat plants at 2, 4 and 6 weeks of growth at 32-27 °C day-night temperatures. The activities are the means of triplicate samples and are counts per milligram dry tissue.

Stage of Growth	Time in minutes after application of P^{32}	OBSERVED COUNTS/MINUTE			Interval between application and counting	COUNTS/MINUTE CORRECTED FOR DECAY		
		Stems	Young leaves	Old leaves		Stems	Young leaves	Old leaves
2 weeks	30	216	83	39	15 days	447	171	80
	60	369	182	104		763	376	215
	90	588	397	306		1218	823	634
	120	905	300	223		1873	621	462
4 weeks	30	245	16	13	17 days	560	37	29
	60	493	203	81		1130	464	186
	90	614	266	479		1407	609	1097
	120	321	162	124		736	371	283
6 weeks	30	143	60	66	5 days	182	76	84
	60	378	75	84		480	95	107
	90	674	81	89		856	103	114
	120	1082	115	95		1374	146	121

TABLE IV. Activity of P^{32} in wheat plants at three temperature regimes. Activity is in counts per minute per milligram dry tissue for the four time periods. The counts for the four time periods were added and divided by four to obtain sample means for 75 minutes.

TEMPERATURE REGIME Day-Night	Age in weeks	Stems	Young leaves	Old leaves
21°-15°C	2	--	--	--
	4	7895	978	439
	6	3718	580	404
27°-21°C	2	6113	2311	921
	4	1045	791	762
	6	467	111	106
32°-27°C	2	1075	498	580
	4	958	370	399
	6	723	105	107

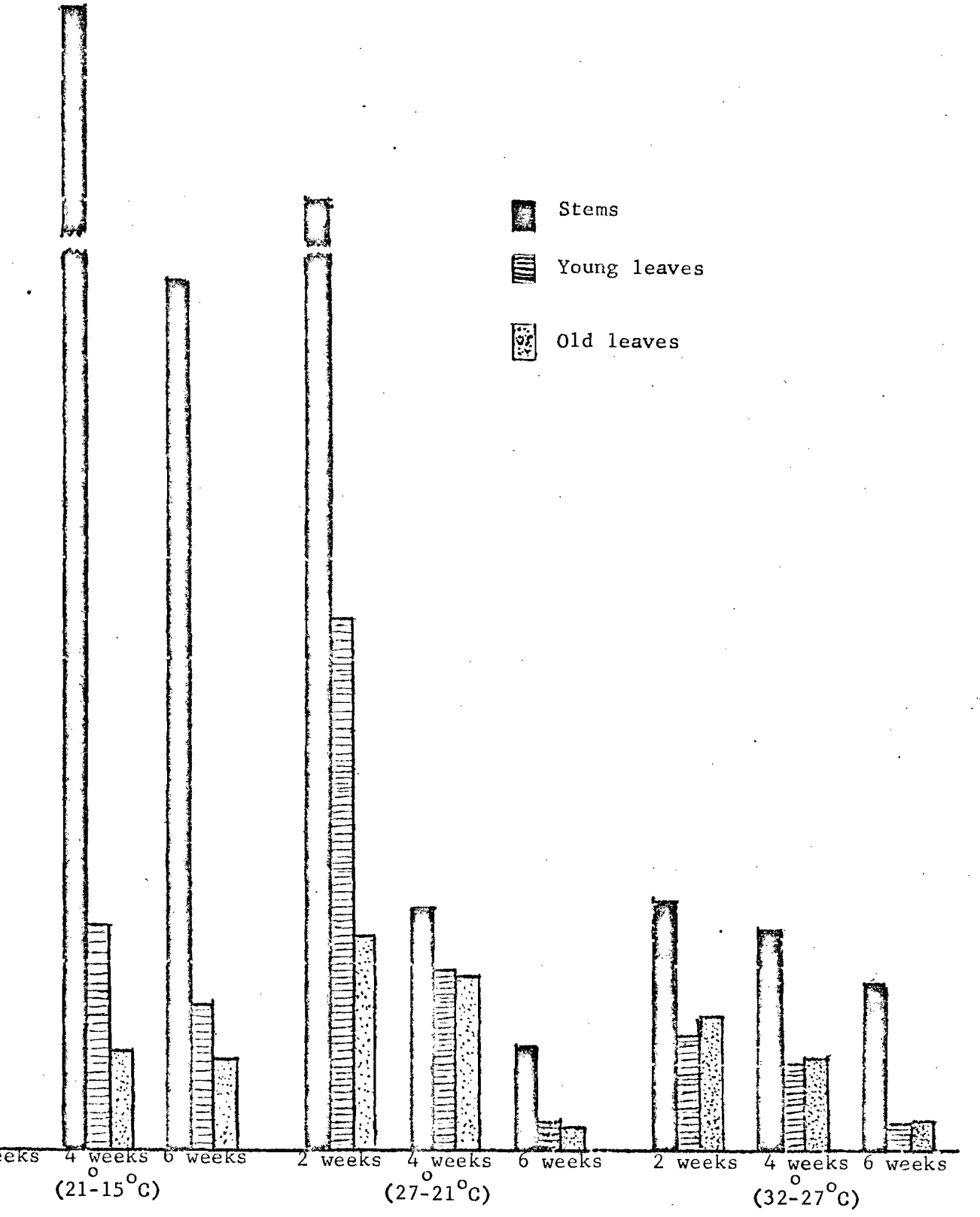

Figure 1. Activity of P^{32} at three temperature regimes.

DISCUSSION

The high activity of radioactive phosphorus in the stem portions of the plants studied, indicate that stems accumulated more phosphorus than any other sampled portion. The higher content of P^{32} in the stems than leaves (both young and old) is probably due to the morphological advantage the stem portion enjoys with respect to plant nutrition. Morphologically, the stem is closer to the source of mineral nutrients than either young or tops of older leaves and the larger xylem vessels of stems contain more nutrients than xylem vessels of leaves. In addition, the sampled stem portions in this study consisted of culms and sheaths, which would indicate more transport network in the stem portion as compared with that found in any of the leaf tissues sampled. Therefore, the stem was in a more favorable position to accumulate P^{32} than young leaves or tops of old leaves.

Young folded leaves accumulated the next highest amounts of P^{32}. This would indicate that, being areas of high metabolic activity, their demand for phosphorus was quite high. But, perhaps, because they were not in a favored position as stems were, they did not equal stems in accumulating P^{32}. Similarly, the tops of the older leaves accumulated the least amount of radioactive phosphorus. However, considering that these were

areas of older tissue, which probably had met their requirements for structure formation, their use of phosphorus was minimal. As Devlin (3) stated that younger leaves will draw on the supply of mineral elements of the older, more mature leaves, then this may agree with the concept that demand for phosphorus in the old leaves was not as high as in the young leaves, in the plants studied.

Results in Fig. 1 illustrate that plants that grew at the lower temperature regime of $21^{\circ}C$-$15^{\circ}C$ (day-night) accumulated more phosphorus than any other plants. Went (16) reported that tomato plants develop an extensive root system at low night temperatures. Although attempts to weigh the root systems of the wheat plants used in the present study were unsuccessful due to entanglement in the sand culture, plants growing at a lower temperature regime may have had more absorptive surface than those at higher temperature regimes.

As the temperature regime was raised, plants accumulated less P^{32}. At the next highest temperature regime of $27^{\circ}C$-$21^{\circ}C$ day-night, the activity of radioactive phosphorus, fell slightly. It dropped noticeably at $32^{\circ}C$-$27^{\circ}C$ day-night temperature. Since other conditions were kept constant, then the variation in temperature might have contributed to reduced absorption of P^{32}. Petinov and Razmaev (10) found that higher temperature slows down the respiration rates in wheat and corn plants. The plants at a higher temperature in this study might have reduced their

respiration rates as a consequence of elevated temperatures, and, therefore, slowed down their uptake of P^{32}. There is evidence that an increase in temperature, inactivates enzyme activity (Molotkovski, 8). With respiration rates reduced and some enzymes made inactive, the demand for phosphorus in plants at higher temperatures would drop --- and thus little P^{32} was translocated upwards.

At all the three temperatures studied, it is seen from the results that the younger stages accumulated more P^{32}. This finding agrees with Roger and Link (11) who found that young alfalfa and oat plants absorb more phosphorus than older ones under the same conditions. This finding implies that wheat plants will take up most of their phosphorus at a younger stage in order to establish themselves.

The results in this experiment show that wheat plants will absorb and translocate less phosphorus at temperature regimes above $27^{o}C$. But they will rapidly absorb phosphorus at temperatures below $27^{o}C$ during the early stages of growth.

From an agriculture standpoint, a successful introduction of such plants as wheat in an exotic environment like Kenya, will require one to pay special attention to temperature requirements and select varieties that will grow optimally within the temperature range of Kenya.

In phosphorus deficient soils, phosphate fertilizers should be applied to the seed bed during planting so that the plants

could take up most of their phosphorus requirements at an early stage.

CONCLUSION

Since the purpose of the experiment was to test the influence of temperature on uptake and translocation of phosphorus, this study has shown that temperature affects accumulation and upward transportation of phosphorus in wheat plants. At lower temperatures, the plants accumulate more phosphorus--most of it in the stems. The stems, however, maintain the highest content of phosphorus at all times.

At temperatures above 27 ^{o}C the plants experience hardships in translocating phosphorus. The plants in the present study responded to a raise in temperature by a decline in radioactive phosphorus content.

Younger plants translocate more phosphorus than older plants at the same temperature regimes. And at higher temperatures, older plants translocated considerably less phosphorus than younger plants.

SUMMARY

Knowledge gained from this study of how temperature affects phosphorus uptake and translocation should guide one in introducing such plants in a new ecological habitat. From the present study, it was learned that temperatures of above 27^{o}C day, and 21^{o}C night reduced the amounts of phosphorus, wheat plants accumulated. But at suitable temperature regime, the plants accumulated more phosphorus during their early stages of growth than older stages. At a temperature regime of 27^{o}C-21^{o}C, two week old plants accumulate more phosphorus than four or six-week old stages.

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