TRANSLOCATION AND DISTRIBUTION OF RADIOACTIVE
PHOSPHORUS IN WHEAT

by

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INTRODUCTION

The discovery of artificial radioactivity and later the
preparation of radioactive isotopes of biologically important
elements has given the plant physiologist a new technique for
studying a number of problems, among them the rate of absorption,
paths of movement, and distribution of inorganic nutrient ele-
ments in plants. Hevesy (9) was the first person to use a radio-
active isotope in a biological tracer experiment. He studied the
uptake of lead by plants using radioactive lead.

Since the discovery of artificial radioactivity, radioactive
phosphorus has been the most extensively applied isotope. This
is largely because it is readily available and possesses char-
acteristics which make it convenient to use as a tracer. In the
present study radioactive phosphorus was used to determine the
time needed for phosphorus to move from the growing medium to the
wheat head, and to show the distribution of phosphorus in the
wheat kernel.

REVIEW OF LITERATURE

Miller (15) in a broad study on the physiology of the wheat
plant at different stages of development found that the amount of
phosphorus in the stems and leaves decreased from a maximum at
heading to a minimum at harvest, while the amount of phosphorus in
the heads increased from their emergence until harvest. He found
the gain of total phosphorus in the head greater than the loss or

gain of this element in the stems and leaves, and stated that apparently a part of the phosphorus migrating into the heads came directly from the soil. In a study of fertilizer uptake in wheat using radioactive phosphorus Spinks and Barber (17) found that there was a large amount of phosphorus uptake by the plant in its later stages of growth but the amount of phosphorus coming from the fertilizer after heading was relatively small. They also observed a transfer of phosphorus from the leaves and stems to the head as the plant approached maturity.

Wood and Sibly (19) in a study on the distribution of zinc in oats found that zinc was absorbed continuously from the growing medium throughout the life cycle of the plant and redistribution of zinc occurred during the development of the inflorescence and grain. They found no zinc translocated from the leaves to other organs, but zinc was supplied to the inflorescence and grain from the roots and the medium. They stated that the greater part of the zinc in the inflorescence and the grain was accounted for by uptake from the medium.

Stout and Hoagland (18) and Arnon et al. (1) have presented evidence to show that movement of absorbed radiophosphorus in the stem is in the transpiration stream. Biddulph (3) stated it is impossible to account for the distribution throughout the plant by any path other than the xylem. He also stated that as the radiophosphorus enters the xylem it is swept into the aerial parts by the transpiration stream. According to Meyer and Anderson (14) "there is no doubt that upward translocation of mineral

salts occurs in the xylem, and it seems virtually certain that
this is the main pathway along which their general upward move-
ment from roots to leaves occurs." Bonner and Galston (4) in
their summary of translocation stated that the mineral elements
absorbed by roots from the soil are transported upward princi-
pally in the transpiration stream of the xylem.

In addition to the movement of absorbed elements within
plants, investigators have studied their distribution within
various plant parts. Harrison et al. (6) made radioautographs
of the kernel of spring wheat which had absorbed radiosulphur
either from the nutrient solution as radioactive sodium sulphate
or from the air as radioactive sulphur dioxide. They found a
marked concentration of sulphur in the embryo and periphery of
the endosperm, particularly in the aleurone layer and cells and
immediately underneath. Additional findings were an appreciable
amount of radioactive sulphur distributed rather uniformly
throughout the interior of the endosperm and a noticeable amount
of activity in the "funicular region in the furrow." The peri-
carp was nearly free of activity.

Arnon et al. (1) made contact radioautographs of transverse
sections of tomato fruit at various stages of development. They
found that fully ripe tomato fruit attached to the vine continued
to absorb small but measurable amounts of phosphorus. This ab-
sorption was limited to the pulp, whereas in green fruit absorp-
tion was marked in both the seed and the pulp. They stated that
this suggests that mineral absorption by the seed ceased at a

definite point in the development of the fruit and shows the importance of the non-seed portion of the fruit as a depot for absorbed phosphorus.

In studies on the composition of the wheat kernel Morris et al. (16) found that the phosphorus content in the peripheral zone of the endosperm was 1.4 and 3.6 times that in the central zone respectively for two varieties of wheat. It was also stated that the phosphorus content of the bran was 18 and 13 times that of the endosperm for the same two varieties. These results were obtained by a spectrographic analysis and reported on a dry weight basis.

In general the results of such studies show there is a differential distribution of inorganic elements within fruits of plants. The method of radioautography serves as an excellent means of showing the location and relative concentration of newly-introduced elements in the various tissues.

The structure and developmental anatomy of the wheat kernel has been studied by many investigators and is extensively reviewed by Hayward (7) and Hector (8). The work presented does not, however, give a critical study on the structure in the area immediately below the furrow. In a study involving the anatomy of cross sections of wheat kernels Bates (2) presented photomicrographs which showed the general structure of the furrow area.

Collins (5), studying the integumentary system of the barley grain, stated that the furrow area corresponded in position and extent with an elongated chalazal tract, through which nutriment

reserve materials passed from the vascular supply in the ovary wall to the cells of the endosperm. He further stated that "the tissue of the pericarp and ovule are continuous; indeed, this elongated tract is to be regarded as the base of the ovule - the extended chalaza - from the flanks of which the integuments originate." A diagram of the furrow area is presented with the chalazal tract and vascular bundle labelled.

Even though the literature gives a general picture regarding the structure of the wheat grain in the area of the furrow (groove, crease) a critical study was not found.

MATERIALS AND METHODS

Experimental Methods

The plants used for experiment one were grown in the green-house. The wheat used was Pusa 52 x Federation, a short season, hard spring wheat from India which has been found to grow extremely well in the greenhouse in Kansas during the winter season. Seeds which were soaked overnight in tap water, were allowed to germinate and grow in vermiculite for one week. Selected seedlings were transferred to quart Mason jars, three plants per jar. Each jar, covered with aluminum paint to exclude light, was fitted with a flat cork (2 3/8" x 5/8", very slight taper) in which four holes had been bored, three for plants and one for an aeration tube. The corks were covered with a thin layer of paraffin to reduce fungus growth. The plants were held in position by means of glass wool.

Hoagland's nutrient solution (10) containing all the essential elements, including the microelements, was used. Additional iron and microelements were added every two days, and distilled water was added as needed to maintain the volume. After one month the plants were transferred to half-gallon Mason jars which were used for the remainder of the growth period. The solution was changed every seven days. Aeration of the nutrient solution was provided by use of glass tubes in each jar connected by a system of rubber tubing to a compressor. A short glass capillary tube, attached to the end of the aeration tube by a rubber connector, was used to prevent a too vigorous agitation of the solution which might have damaged the roots.

Supplementary illumination was provided on cloudy days by a bank of sixteen, 40 watt, white, fluorescent lamps 48 inches in length. This light source provided about 1,000 foot candles at a distance of one foot, as measured with a Weston Sunlight Meter. A temperature of 70 $\pm$ 10° F. was maintained during the growth period. Fungus growth on the lower surface of the cork lids was checked by periodically painting with a 1:1000 $HgCl_2$ solution. The plants were found to grow extremely well under these conditions obtaining heights of about 1, 2, and $3\frac{1}{2}$ feet after 6, 8, and 14 weeks respectively (PLATE I). The flowering date of each head was recorded on a tag attached to the culm.

The plants used for experiment two were grown in a field plot on the Agronomy Farm. The wheat used was a hard red winter variety, Pawnee, planted October 27, 1953. The flowering date of each of several heads selected at random was recorded on a tag attached

EXPLANATION OF PLATE I

A - Age 6 weeks - height 1 foot.

B - Age 8 weeks - height 2 feet.

C - Age 14 weeks - height $3\frac{1}{2}$ feet.

PLATE I

to the culm.

Radiophosphorus Used

The radiophosphorus used was P^{32}, obtained from the Oak Ridge National Laboratory in the form of phosphate in weak hydrochloric acid (acidity less than 0.5 normal). In its preparation, ordinary sulphur was bombarded with neutrons in the uranium pile reactor according to the reaction, $S^{32}(n,p)P^{32}$. This method produced an isotope with a high specific activity ($\sim 0.025 mgP/mcP^{32}$) and a radiochemical purity of more than 99 percent.

The radioactive isotope P^{32} has convenient characteristics for use as a biological tracer. Upon decay a beta particle with a maximum energy of 1.71 mev is emitted (12), thus permitting use of a thin window Geiger-Muller tube for counting. Beta particles are effective for radioautography in that they are absorbed in the film emulsion. The absence of gamma radiation allows the investigator to handle the material without having to resort to extreme precautions for external protection. The half life of 14.30 days (12) is short enough that disposal problems are not difficult and long enough for the investigator to carry out his experiment without undue haste.

Method and Time of Application of P^{32}

To reduce disposal problems the greenhouse plants were transferred from the half-gallon jars to pint Mason jars in which 200 ml of nutrient solution was placed and two of the three plants and all but the selected culm of the third plant discarded. By means

of a micropipette P^{32} was added to give a value of 80-90 micro-
curies in the 200 ml of nutrient solution. Field plants, after
being dug from the ground, the soil washed from the roots, and all
but the selected culm discarded, were placed in a pint jar con-
taining 200 ml of nutrient solution and about 100 microcuries of
P^{32} added by means of the micropipette.

Selected culms were used at weekly intervals, with respect
to their flowering dates, starting one week after flowering for
culms of greenhouse plants, and two weeks after flowering for
culms of field plants.

Method of Detecting P^{32} in the Wheat Head

To detect P^{32} in the wheat head a thin window Geiger-Muller
tube was placed in a horizontal position next to the mid-region of
the head. The tube was attached to a scaler circuit which record-
ed counts per unit of time (PLATE II). Readings were taken every
half hour. Corrections were made for background and all counting
was done in the greenhouse. Counting of dissected parts was done
with a Geiger-Muller tube enclosed in a lead chamber and attached
to a scaler circuit. Corrections were made for background.

Preparation of Radioautographs

Radioautographs were prepared by pressing sections of
kernels in close contact with the film during exposure. P^{32} was
allowed to accumulate in the head until ~5,000 counts per minute
for greenhouse grown plants and ~9,000 counts per minute for
field grown plants were obtained. Kernels were dissected from
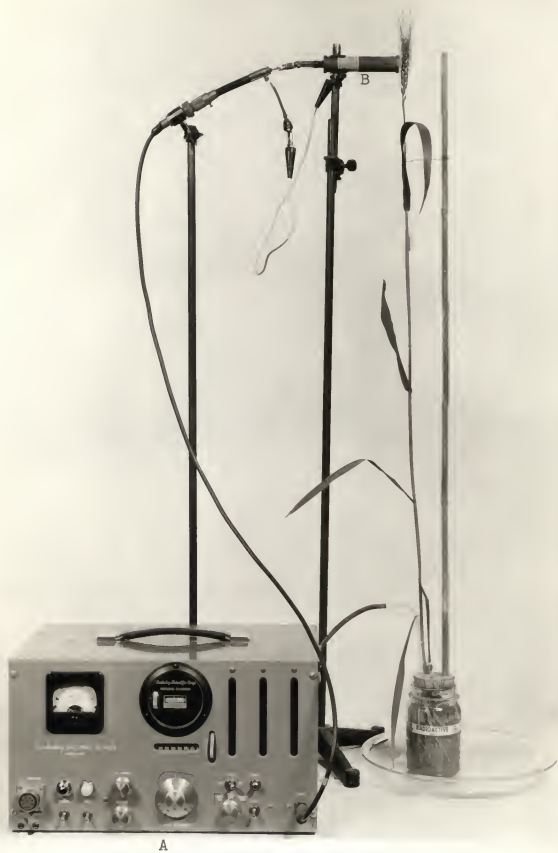the florets and sliced into cross and longitudinal sections

EXPLANATION OF PLATE II

Method of detecting P^{32} in the head.

A - Scaler circuit.

B - Thin window Geiger-Muller tube.

PLATE II

(250 microns thick) with a hand microtome. The sections were placed serially in rows on a strip of polystyrene (thickness 0.025 mm, density $2.657 mg/cm^2$) lying in an ordinary cigar box. Another strip of polystyrene was placed over the sections over which was placed a photographic or X-ray film. The film was covered with a piece of bakelite sheet, one-fourth inch thick, and a small lead weight. The box was closed and wrapped in a black cloth to exclude light. The exposure time was calculated after determining the number of disintegrations per second per square centimeter of the cross sections. Eastman no-screen X-ray film was used for the sections of kernels from greenhouse plants and Eastman Portrait Panchromatic film was used for the sections of kernels from field plants. The films had exposure times of 5×10^7 and 1.4×10^8 disintegrations per square centimeter respectively (13).

The film was developed by ordinary processes using Kodak X-ray developer for the no-screen X-ray film, and Kodak D-50 developer for the Portrait Panchromatic film. Kodak F-5 fixing solution was used for both types of film.

Preparation of Sections

After shaving off the ends, the kernels were treated two hours in absolute ethyl alcohol for killing and fixing. They were prepared for embedding by treating in each of the following: absolute ethyl alcohol-tertiary butyl alcohol, 2:1, three hours; absolute ethyl alcohol-tertiary butyl alcohol, 1:1, overnight;

absolute ethyl alcohol-tertiary butyl alcohol, 1:2, three hours; and two changes of pure tertiary butyl alcohol, the first three hours and the second allowed to remain overnight.

The infiltration and embedding in Tissuemat (Fisher, M. P. 56-58) was done as described under Paraffin Methods, Dehydration with Tertiary Butyl Alcohol by Johansen (11). The blocks were left in water until time of sectioning. When difficulties were encountered, the paraffin was cut away at one end and the kernel left in water for a few hours longer. Sectioning was done with a rotary microtome, using a safety razor blade. The pieces were placed on clean slides, the paraffin removed with xylol, stained lightly with safranin, and mounted in balsam.

EXPERIMENTAL RESULTS

Part I. Time Required for P^{32} to Reach the Head

Experiment one was conducted on greenhouse plants. The culms used were selected with heads at stages of one, four, and five weeks after flowering. For the time recorded, the presence of P^{32} in the head was five times background or more. Results are given in Table 1.

Experiment two was conducted on field plants. The culms used were selected with heads at stages of two, three, four, and five weeks after flowering. For the time recorded, the presence of P^{32} in the head was five times background or more. Results are given in Table 1.

Table 1. Time required for P^{32} to reach the heads of greenhouse and field plants.

Culm (where grown)	Stage (weeks after flowering)	Height to middle of head (cm)	Time required for P^{32} to reach head (min)
Greenhouse	1	84	60
"	4	88	60
"	5	97	90
Field	2	80	60
"	3	60	30
"	4	72	60*
"	5	66	(see text)

* It was found, after dissection of the parts, the P^{32} in this head was located in the chaff and not in the kernels.

The leaves were removed from the culm bearing a head at a stage of four weeks after flowering. P^{32} was detected only in the basal portion of the flag leaf and the chaff of the head. It was present, however, in the entire length of the stem. No P^{32} was detected in any part of a culm with a head at a stage of five weeks after flowering.

Part II. Distribution of P^{32} in the Kernel

Experiment one was conducted on greenhouse plants. Culms were selected with heads at stages of one, four, and five weeks after flowering. Radioautographs of sections of the kernels were obtained with exposures of 30-36 hours. Results are given in PLATES III, IV, and V. A comparison of the radioautographs indicated that the greater concentrations of P^{32} are in the embryo, the area immediately below the furrow, and in the bran

EXPLANATION OF PLATE III

Radioautographs of kernels from greenhouse plants one
week after flowering. Pairs of serial sections (x4).

Figs. 1 and 2. Longitudinal sections cut
          perpendicular to the furrow.

Fig. 3. Longitudinal sections cut parallel
        with the furrow.

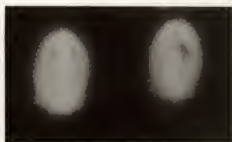Fig. 4. Cross sections.

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PLATE III
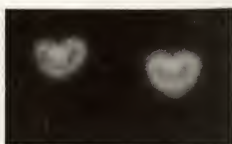

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE IV

Radioautographs of kernels from greenhouse plants four
weeks after flowering. Pairs of serial sections (x4).

    Fig. 1. Longitudinal sections cut parallel
             with the furrow.

    Figs. 2 and 3. Longitudinal sections cut
             perpendicular to the furrow.

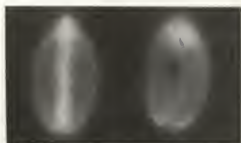   Fig. 4. Cross sections.

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PLATE IV

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE V

Radioautographs of kernels from greenhouse plants five
weeks after flowering. Pairs of serial sections (x4).

Fig. 1. Longitudinal sections cut parallel
          with the furrow.

Figs. 2 and 3. Longitudinal sections cut
          perpendicular to the furrow.

Fig. 4. Cross sections.

PLATE V

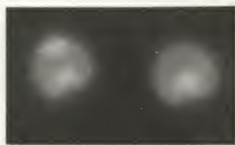
Fig. 1

Fig. 2

Fig. 3

Fig. 4

layers. The bran layers here are interpreted as including the parietal aleurone. The concentration in the bran layers appeared to decrease in the later stages of development. The endosperm showed a quite uniform concentration of P^{32} in all stages of development with a relatively heavier concentration in the very young stage. Plate III, Fig. 1, shows a separated pericarp containing a high concentration of P^{32}.

Experiment two was conducted on field plants. Culms were selected with heads at stages of two, three, four, and five weeks after flowering. No P^{32} entered the kernels of heads at stages of four and five weeks after flowering. Radioautographs of sections of the kernels at stages of two and three weeks after flowering were obtained with exposures of 200-250 hours. Results are given in PLATES VI and VII. Comparison of the radioautographs indicated that the greater concentrations of P^{32} are in the bran layers, the area immediately below the furrow, and in the embryo. The concentration in the bran layers appeared to decrease slightly in the later stage. The endosperm showed a quite uniform concentration of P^{32}.

Part III. Structure of the Area Immediately Below the Furrow

From the results observed in the radioautographs of Part II it was deemed desirable to investigate the structure of the kernel in the region immediately below the furrow. Kernels of greenhouse plants at a stage of about four weeks after flowering were used. Photomicrographs were obtained from sections 25-30

EXPLANATION OF PLATE VI

Radioautographs of kernels from field plants two weeks
after flowering. Pairs of serial sections (x4).

Figs. 1 and 2. Longitudinal sections cut
perpendicular to the furrow.

Figs. 3 and 4. Cross sections.

PLATE VI

Fig. 1

Fig. 2

Fig. 3

Fig. 4

EXPLANATION OF PLATE VII

Radioautographs of kernels from field plants three weeks
after flowering. Pairs of serial sections (x4).

      Fig. 1. Longitudinal sections cut parallel
             with the furrow.

      Figs. 2 and 3. Longitudinal sections cut
             perpendicular to the furrow.

      Fig. 4. Cross sections.

PLATE VII

Fig. 1

Fig. 2

Fig. 3

Fig. 4

microns thick. Results are given in PLATES VIII, IX, and X.
Shown is the funiculus containing vascular and parenchymatous
tissue, the chalazal tract lying between the points of origin
of the integuments, and the aleurone layer which constitutes the
outermost layer of the endosperm.

DISCUSSION

Miller (15) suggested that a part of the phosphorus migrating
into the heads of wheat during their development came directly
from the soil. Culms from both greenhouse and field plants
studied in this respect showed an upward movement of P^{32} into the
heads at rates of at least 80 centimeters per hour for four
culms and at least 64 centimeters per hour for two. Assuming
that it is impossible for P^{32} to move into the vegetative tissue
of stem and leaf, pass through the metabolic pool, and be re-
distributed into the head in this time interval, indications are
that the P^{32} moved in the transpiration stream from the medium
directly into the head. This condition occurred in all the culms
tested which took up P^{32}.

Further evidence was given by the culm of the field plant
studied at the late stage of development. It had P^{32} in the full
length of the stem, the chaff of the head, and the basal portion
of the flag leaf. The other leaves, which were dead, contained
no P^{32}. The absence of P^{32} in the leaves indicates that it moved
in the transpiration stream from the medium directly into the
chaff of the head.

EXPLANATION OF PLATE VIII

Structure of the area immediately below the furrow (x95).

A - Pericarp
B - Funiculus
C - Chalazal tract
D - Integuments and nucellus
E - Lacuna
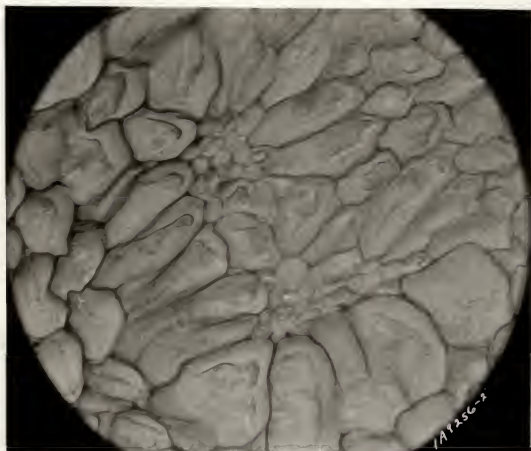F - Aleuron layer
G - Endosperm

PLATE VIII
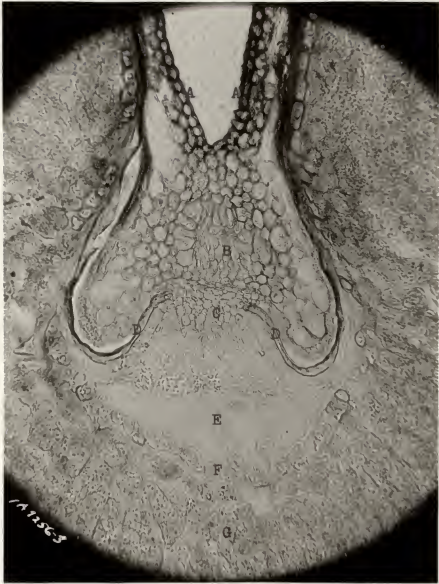
EXPLANATION OF PLATE IX

Enlargement of the funiculus (x520).
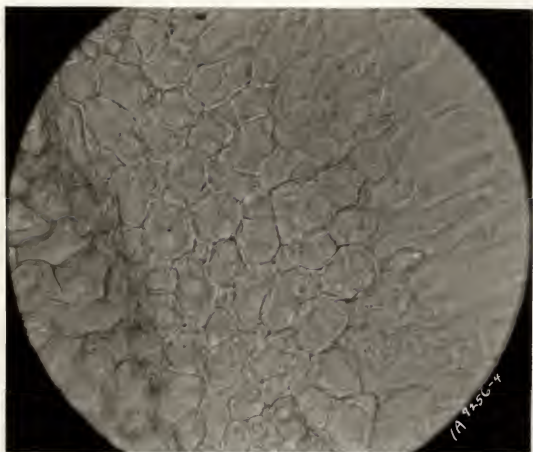
Note the two vascular bundles.

PLATE IX

EXPLANATION OF PLATE X

Enlargement of the chalazal tract (x520).

PLATE X

Radioautographs of both longitudinal and cross sections showed that there was a differential distribution of P^{32} in the wheat kernel. Greater concentrations were found in the embryo, the area immediately below the furrow, and the bran layers. The endosperm showed a quite uniform concentration. The concentration in the bran layers appeared to decrease in later stages of development, which gives indication that distribution of P^{32} to the bran layers, which includes the aleurone, was more marked in the early stages. The results for both greenhouse and field plants were approximately the same. In general, these results were similar to those of Harrison et al. (6) using radioactive sulphur.

The failure of kernels from field plants to take up P^{32} four weeks after flowering showed that no phosphorus is taken up by kernels after they are ripe. Field wheat was judged by the station plant breeder to be ripe 26-28 days after flowering.

The high concentration of P^{32} in the area immediately below the furrow at all stages of development was accounted for by the presence of the funiculus with its vascular bundles and the chalazal tract. Through these structures pass nutriment and reserve materials to the developing seed.

Photomicrographs obtained from the area immediately below the furrow showed that this area in the wheat kernel was similar in structure to that of the barley grain as observed by Collins (5).

SUMMARY

Studies on the translocation and distribution of phosphorus in the wheat plant were conducted with P^{32}.

Evidence was obtained that P^{32} moved in the transpiration stream from the medium directly into the head.

No P^{32} was taken up by the kernels after they were ripe.

There was a differential distribution of P^{32} in the kernel with greater concentrations in the embryo, the bran layers including the aleurone, and the conducting area immediately below the furrow.

A careful study indicated that the structure of the area of the wheat kernel immediately below the furrow is concerned with distribution of reserves to the developing seed.

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The purpose of this study was two-fold: (1) to determine whether any of the phosphorus moving into the wheat head came directly from the medium without passing through the metabolic pool of the plant, and (2) to show the distribution of phosphorus in the wheat kernel.

Wheat was grown both in the greenhouse and in the field. That in the greenhouse was a spring variety, Pusa 52 x Federation, while in the field a winter variety, Pawnee, was grown. Culms were selected at weekly intervals starting one week after flowering for greenhouse plants, and two weeks after flowering for field plants. At the time of testing, P^{32} was added directly to the nutrient solution in which the greenhouse plants were growing. The field plants were excavated, soil washed from the roots, and transferred to nutrient solution containing P^{32}. The time of P^{32} uptake in the head was determined by a Geiger-Muller tube placed next to it. In addition radioautographs were prepared by pressing sections of kernels in close contact with a photographic or X-ray film for exposure.

It was found from both greenhouse and field plants studied that there was an upward movement of P^{32} into the heads at rates of at least 80 centimeters per hour for four culms and at least 64 centimeters per hour for two. Assuming that it is impossible for P^{32} to move into the vegetative tissue of stem and leaf, pass through the metabolic pool, and be redistributed into the head in this time interval, indications are that the P^{32} moved

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the area immediately below the furrow, and in the bran layers.
The bran layers here are interpreted as including the parietal
aleurone. The endosperm showed a quite uniform concentration.
The concentration in the bran layers appeared to decrease in
later stages of development, giving indication that distribution
of P^{32} to the bran layers, including the aleurone, was more
marked in the early stages. The results for both greenhouse and
field plants were approximately the same.

From the results observed in the radioautographs it was
deemed desirable to investigate the anatomical structure of the
kernel in the area immediately below the furrow. Kernels were
embedded in paraffin and sectioned with a rotary microtome. A
careful study of the sections indicated that this structure is
concerned with distribution of reserves to the developing seed,
thus accounting for the high concentration of P^{32} in this area.