The Uptake of Na^{22} by Intact Plants as Related to Root-to-Shoot Weight Ratio[1]

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INTRODUCTION

The understanding of ion absorption by plants is essential to the solution of the physicochemical processes involved in plant growth. One consideration is the mechanism, pathway, and amount of nutrients that plant cells can accumulate against an electrochemical potential gradient from an external environment.

Two phases of uptake have been recognized by many authors (*1,2,5*)[3]: an initial rapid uptake, followed by a period during which the amounts absorbed are a function of time. Epstein and Legget's (*2*) work is worth mentioning here because of their presentation of reasonable evidence on the existence of these two phases. The evidence presented is consistent with the view that the initial phase has characteristics of cation-exchange adsorption, the equilibrium of which is essentially completed in 30 minutes. They worked with labeled strontium, and after 60 minutes, by replacing the bathing solution with the same unlabeled element at the same concentration, a desorption of labeled strontium occurred, the time course of which resembled the initial uptake. Though a large part of the radioactive strontium taken up initially was readily exchangeable with ambient strontium, a fraction was not subject to rapid exchange, and further release was negligible, as shown by a nearly horizontal trend of the second part of the curve.

However, Epstein and Legget's studies were carried out with excised barley roots, probably because the objective was to investigate the trend of salt accumulation rather than the involving influence of nutritional factors and physiological processes going on in an intact plant, which add complexity to the mechanism of mineral absorption.

It is possibly true that some aspects of the mechanism of mineral uptake by root cells can be studied most simply by eliminating, during the experimental period, the influence of root-and-shoot relationships. Kramer (*3*)

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[3] Italic numbers in parentheses refer to Literature Cited, p. 279.

pointed out, with reference to the statement that absorption occurs principally on the meristematic region of the roots, that it is based largely on studies of salt accumulation in the cells of excised roots, rather than on measurements of absorption through the roots of intact, actively transpiring plants.

The present study was carried out to investigate whether the time-course uptake of Na^{22} by intact plants follows a trend similar to that of excised roots. It was also planned to investigate uptake and desorption with respect to the root-to-shoot weight ratio, a factor which may be visualized as reflecting the photosynthetic, energetic, and metabolic activity in an intact plant.

EXPERIMENTAL METHODS

LABORATORY PROCEDURE

From a bunch of around 80 corn seedlings 10 days old, grown in nutrient solution with forced aeration, 60 apparently healthy plants were selected for the experimental procedure. Precautions were taken to avoid damage to the roots, the length of which ranged from around 15 to 30 cm. The seedlings were next placed with their roots immersed in 0.1-concentration Hoagland's Solution for about 15 minutes before the zero time of the experiment started.

A time-course uptake of Na^{22} was outlined for exponentially increasing periods of 10^0, $10^{\frac{1}{2}}$, . . . 10^3 minutes. The bathing solution contained 10 μc of Na^{22} in 1 liter of 0.1-strength Hoagland's solution. One intact plant was removed from the solution at the end of each of the above-indicated absorption periods. After removal of each plant the immersed roots were rinsed for about 2 seconds in distilled water and separated from the shoots at the base of the hypocotyl. Both sections, roots and shoots, were then carefully placed inside test tubes properly identified.

At the end of 10- and 100-minute periods nine other seedlings were removed in addition to the corresponding one. This was done to follow as well a time-course of desorption with increasing time. The nine seedlings were treated as follows: Five seedlings were placed in 0.1-strength Hoagland's solution containing 0.005-M. (molar) NaCl. At the end of 1, 3.2, 10, 32, and 100 minutes, one plant was rapidly removed and the same procedure was followed, placing roots and shoots separated in identified test tubes. Three other plants were placed in distilled water for 1, 10, and 100 minutes, and a last plant was placed in 0.1-strength Hoagland's solution for 100 minutes, these too being handled like the previous seedlings.

The experimental work was replicated twice. One-milliliter aliquots were removed from the radioactive solution at the end of 1, 100, and 1,000 minutes to check whether any change in Na^{22} concentration occurred during the course of the experiment.

The separated roots and shoots of 11 healthy seedlings, also selected from those remaining in the bunch, were weighed green. Their dry weight was also determined. The mean weight of the 11 roots and shoots, green and dry, was determined to derive a dry- to green-weight conversion factor, and present the results on the basis of fresh weight of plant material. The dry weight of all the experimental material in the test tubes was determined for this purpose.

COUNTING PROCEDURE

The roots and shoots, separated in test tubes of the proper size, were counted for γ emission of Na^{22} in a scintillation-counter consisting of a spectrometer with an electronic sweep and a scaler connected to a precision timer. This provided for an efficient detection of rays. All samples were corrected for background and the results were all calculated to read in counts per minute.

Count rates were also made for the 1-ml. samples obtained from the radioactive solution at the end of 1, 100, and 1,000 minutes. The mean count rate was 9,525 per minute, and the highest deviation was found to be within 3½ percent of the mean.

RESULTS

The time-course uptake of Na^{22} with exponentially increasing periods is presented in table 1 for the two replications. It is apparent from figure 1 that the uptake of labeled sodium by intact corn plants was still increasing exponentially after 16.67 hours (1,000 minutes), though in some instances it approached a saturation point. Shoot uptake also increased somewhat exponentially with time after the first 10 minutes (table 1). It appeared to be dependent on root uptake, although independent of root-to-shoot weight ratio. However, where values of this ratio exhibited greatest deviations from the mean, an inverse relationship existed with respect to the trend of uptake of Na^{22} by the intact plants with time.

The results obtained for the time-course of desorption of labeled sodium after 10 and 100 minutes are summarized in table 2. The shoot apparently exhibited little or no leaching with time, irrespective of leaching solution. The results are rather inconclusive with respect to the shoot. However, the trend of desorption of roots plus shoot with time appears again to be affected by extreme values of root-to-shoot weight ratio, this time in a direct manner. The limited results obtained with distilled water and Hoagland's solution as leaching solutions give no assistance in comparing desorption with and without the presence of exchangeable ions.

TABLE 1.—*Time-course of uptake of Na^{22} by individual corn seedlings, as indicated by their γ-ray emission in counts per minute*

Exposure time (minutes)	Counts per minute (background corrected)				Root-to-shoot weight ratio	
	Root plus shoot, per gram fresh weight of root		Shoot—total activity			
	First replication	Second replication	First replication	Second replication	First replication	Second replication
1	1	—	880	--	0.42	0.51
3.2	11	9	1,130	884	.26	.44
10	13	14	1,156	1,610	.73	.41
32	62	361	4,710	6,890	.29	.38
100	289	600	6,170	7,450	.33	.53
316	560	866	14,760	11,120	.39	.47
1,000	6,924	5,124	84,500	45,200	.33	.48

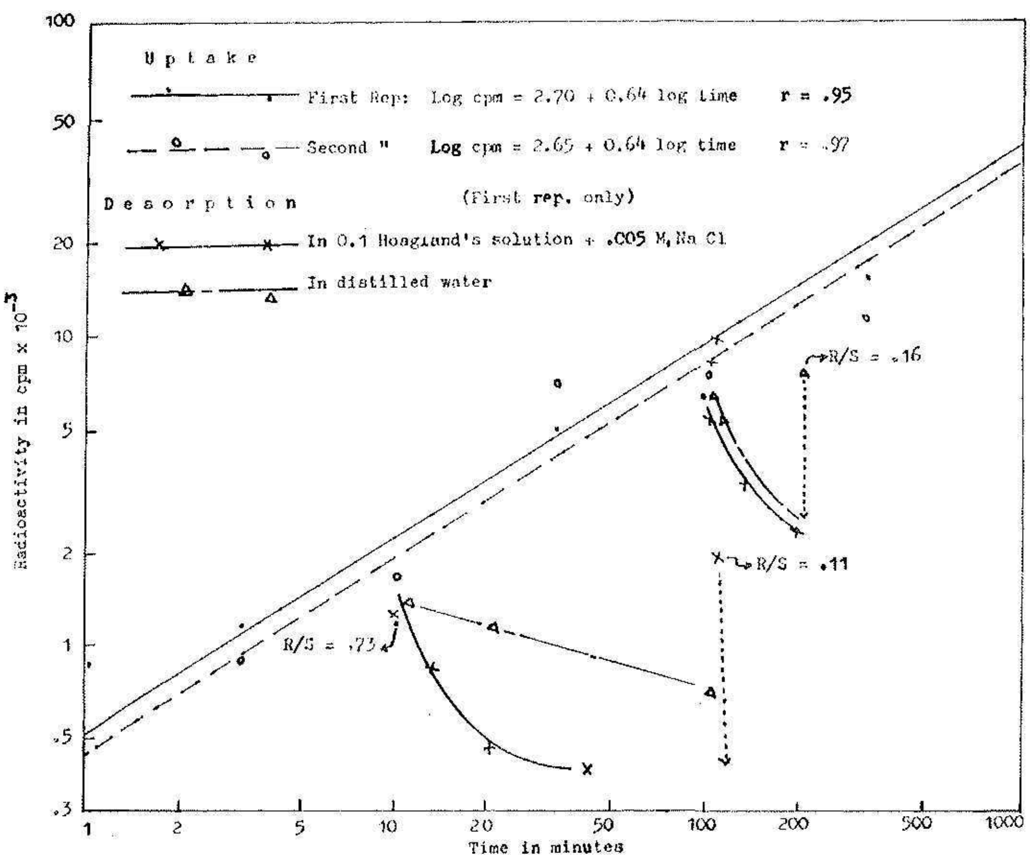

FIG. 1.—The time-course of uptake of Na^{22} by corn seedlings, determined by log-log linear regression analysis. The time-course of desorption trends, after 10 and 100 minutes, are also indicated. Rep. = replication; cpm = counts per minute.

The time-course of desorption of Na^{22} by the corn seedlings is also presented graphically in figure 1 for the first replication to visualize better the actual nature of uptake and desorption with time. The curve describing desorption of Na^{22} with respect to time, after 10 minutes of root exposure to the labeled ion, is fairly well defined, except for the seedling leached for

TABLE 2.—*Time-course of desorption of Na^{22} by individual corn seedlings, as obtained by leaching of the labeled element with different solutions, after 10 and 100 minutes exposure of the roots to the labeled bathing solution*

Leaching time (minutes)	Counts per minute (background corrected)								Root-to-shoot weight ratio			
	Root plus shoot per gram fresh weight of root				Shoot, total activity							
	Counts per minute (background corrected) after—											
	1st replication		2nd replication		1st replication		2nd replication		1st replication		2nd replication	
	10 min.	100 min.	10 min.	100 min.	10 min.	100 min.	10 min.	100 min.	10 min.	100 min.	10 min.	100 min.
	Leaching solution—0.1 Hoogland + 0.005 NaCl											
1.0	3	532	66	734	1,189	8,370	1,840	13,595	0.24	0.27	0.32	0.33
3.2	0	242	50	72	837	5,290	1,708	6,020	.39	.28	.38	.35
10	15	296	116	676	447	9,625	1,130	8,065	.56	.24	.34	.45
32	22	70	74	994	389	3,287	1,268	11,340	.32	.41	.31	.26
100	40	115	70	349	1,915	2,263	647	5,750	.11	.52	.47	.53
	Leaching solution—distilled water											
1	6	186	11	834	1,300	6,370	2,478	8,170	0.38	0.36	0.30	0.34
10	9	232	33	404	1,089	5,150	1,294	3,735	.35	.32	.30	.61
100	14	208	97	510	673	7,525	1,079	4,542	.35	.16	.34	.54
	Leaching solution—0.1 Hoogland solution											
100	7	399	63	1126	554	3,505	541	4,340	0.35	0.43	0.46	0.56

100 minutes. The amount of Na^{22} leached in this particular case was the least, despite the seedlings being bathed for the longest period. The best possible explanation of this low leaching appears to reside in the abnormally low root-to-shoot weight ratio. In fact, it was the lowest of all the experimental material. Otherwise, this desorption curve appears to suggest a rapid desorption followed by a steady desorption phase.

In general, it appears that under the experimental conditions, those seedlings having the lowest root-to-shoot weight ratios exhibited greater uptake and less desorption from the complete plant per gram of fresh-weight root. On the other hand, seedlings with the highest values of this ratio behaved oppositely.

In an attempt to relate root-to-shoot weight ratio with uptake and absorption trends with time, the expected values of uptake and desorption with time were calculated by log-log linear regression. This analysis was made separately for the first and second replications of uptake, as well as for the first and second replications of leaching with Hoagland's solution with ambient sodium ions, started after 10 minutes of exposure to the labeled bathing solution. Linear regression was not significant to produce reliable expected values for the rest of the data.

There appears to exist, as indicated by figure 2, a significant relationship between the ratio of expected to actual counts per minute (cpm) of labeled sodium present in the intact plants, on a per-gram fresh-weight root basis, and their root-to-shoot weight ratio. This functional relationship remains valid for both uptake and desorption phases of the intact plants. Values of both ratios increase directly proportional to each other, as given by the regression equation describing figure 2. This implies that, as the fresh weight of roots for a given seedling increases with respect to its shoot, the specific activity of Na^{22} is less than that of the expected value for the given time-course trend of either uptake or desorption. Thus, under conditions of a high absorbing surface, not balanced accordingly by shoot volume, a given intact plant generally indicated less uptake (less radioactivity) and greater desorption (less radioactivity) than a seedling with or near a root: shoot ratio of around 0.39, which was the mean value of the experimental plants. It is rather interesting to note that by the equation

$$\frac{\text{Expected cpm}}{\text{Actual cpm}} = 0.28 + 1.85\ R/S$$

representing the linear regression equation of figure 2, when R/S is substituted by the mean value of this ratio, for the experimental material used, the ratio of expected to actual counts per minute is unity.

DISCUSSION

The questions to which answers were sought in this experiment may be summarized as follows: 1, Do intact plants absorb and accumulate ions as found with excised roots, that is, make a rapid initial uptake whose equilibrium is essentially attained in 10 minutes, this followed by a steady accumulation phase? 2, Is mineral accumulation in the shoot, or in the intact plant, a root-dependent function, that is, is a root-and-shoot pathway for accumulation in series, or in parallel?

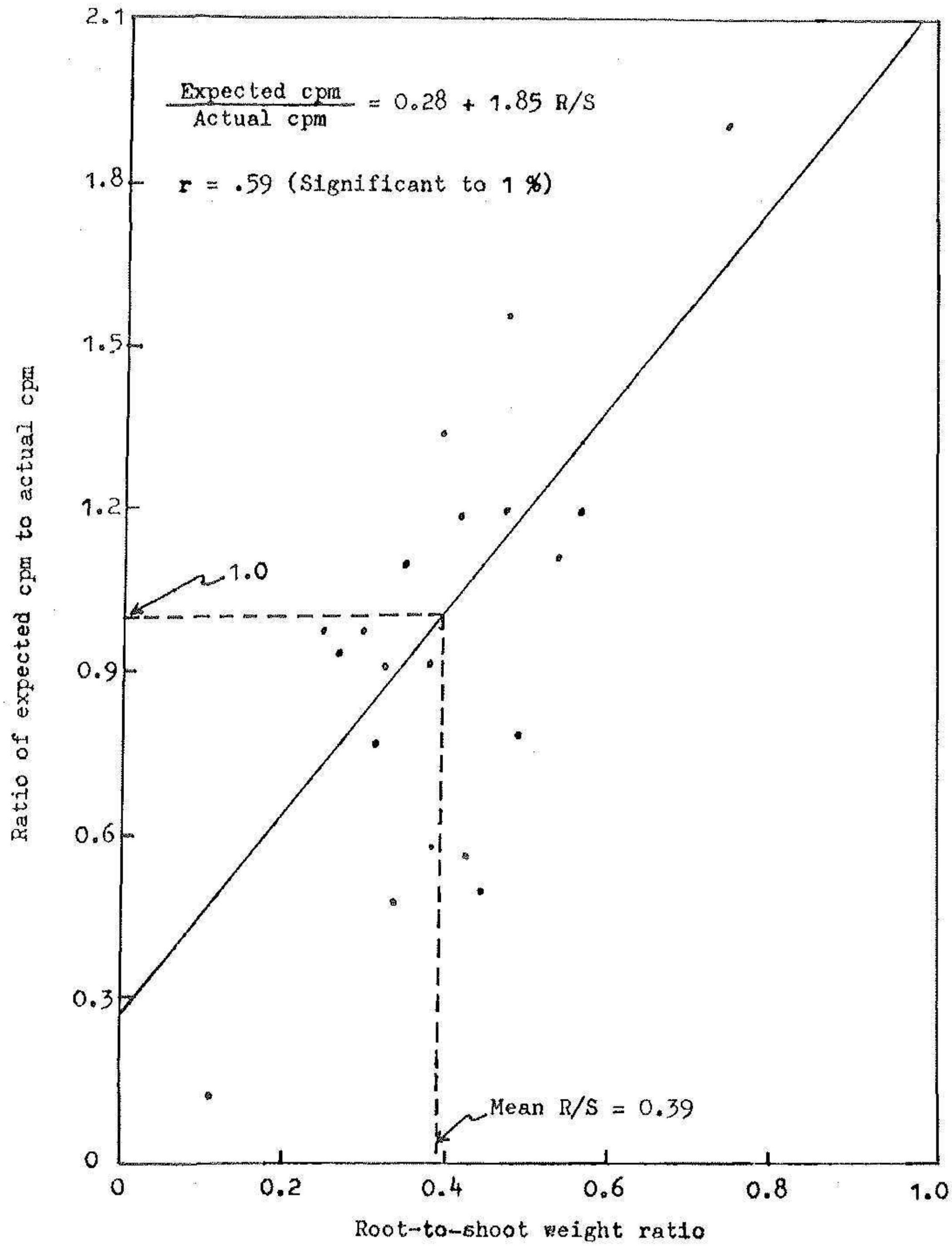

FIG. 2.—The ratio of expected to actual values of uptake and desorption, as a function of the root-to-shoot weight ratio of the corn seedlings.

The influence of a continuous supply of substrate material to the roots from the aerial parts in the plant, which may include carriers to a point of entry against a concentration gradient, appears to alter the uptake and accumulation pattern obtained by various investigators when working with excised roots. However, the results here obtained do not offer conclusive evidence because of experimental uncertainties. For example, the time used in rinsing the roots of seedlings after completion of exposure time in the labeled solution was more critical than was expected. For short-time exposure periods (1, 3.2, and 10 minutes) 2-second rinsing is different from 3. Also, the environmental conditions influencing respiration and transpiration rates of the experimental material along the duration of each replicate may have differed somewhat.

The high, off-trend values of specific activity obtained in both phases of uptake and desorption of labeled sodium are apparently connected with the shoot. All the seedlings with extremely low values of root-to-shoot weight ratio exhibited either greater than expected uptake or less than expected desorption, per gram of fresh-weight root. On the other hand, the greater R/S values tended to be associated with lower than expected uptake or greater than expected desorption. The supply of carriers or carrier substrates from the shoot to a point of entry in the roots—as an active component, or transpirational pull—as passive component, or both, may largely account for the significant relationship shown in figure 2. As a low R/S ratio leads to a divergent condition with respect to transpiration, which may imply reduced transpiration rates, uptake and transpiration would not relate well.

The possibility exists that an active, rate-dependent transport mechanism originating in the shoot, may serve as a better explanation for the relationship given by figure 2. The computation of results in terms of specific activity minimizes the quantitative influence of the roots, as component in the root-shoot ratio, on uptake or desorption trends. An intact plant with low root-to-shoot weight ratio may be considered to have a more efficient active transport mechanism. It is probably less rate-dependent with respect to the downward supply of carriers or respiration substrates. Respiration is necessary to provide the energy of accumulation (*1*). On the other hand a plant with a high root-to-shoot ratio is probably more rate-dependent with respect to respiration substrates, and thus is provided with a less efficient active transport mechanism. Mineral translocation by mass flow along the transpiration stream may become more active in this case. This may give rise to a convergent condition, and if the plant is allowed to undergo desorption, leaching would proceed more freely due to greater "congestion" in the "free space". The limited results of this experiment support these views.

The variable weight of roots of the intact plants presents a problem not accurately solved by expressing the activity on a per-gram, fresh-weight basis. Kramer (*4*) and Kramer and Wiebe (*5*) found that absorption rates varied along longitudinal sections of the roots and were not limited to the meristematic region, though gradients actually occur.

As to whether accumulation in the shoot is "in series" or "in parallel" with accumulation in the roots, the former appears to be more likely, in contrast to Epstein's (*2*) postulate that shoot accumulation is "in parallel" with that in the roots.

The results of this experiment have a bearing on the management of clipped pastures. After harvest, a given stand is at its upmost root-to-shoot ratio, and thus, mineral nutrition is liable to be critical. The height of clipping enters here as an important factor. If clipping is carried during days of high rainfall, waterlogged conditions may prevail for some days, and the situation worsens due to low oxygen content and low temperature around the roots, conditions not proper for normal respiration.

SUMMARY

A laboratory study was made to investigate the time-course uptake of Na^{22} by intact plants. The time-course desorption of labeled sodium was also investigated after two exposure periods, while the uptake course in a bathing solution was going on.

A significant relationship was obtained for the ratio of expected to actual values of uptake and desorption as a function of the root-to-shoot weight ratio. By expressing the activity on a per-gram fresh-weight root basis (specific activity) it appears that low values of root-to-shoot ratio are associated with greater than expected values of uptake and greater than expected values of desorption. The opposite is generally obtained with respect to extreme high values of the root-to-shoot ratio.

The predominance of active transport as an accumulation mechanism is suggested when low root-to-shoot ratio values characterize the intact plants. High ratios would favor translocation by way of passive mass-flow along the transpiration stream.

RESUMEN

Se realizó un estudio en el laboratorio para reconocer la tendencia de absorción del Na^{22} por plántulas de maíz, en función de tiempo. Simultáneamente, también se estudió la deabsorción del sodio marcado en función de tiempo, luego de dos períodos fijados de absorción.

Se obtuvo una relación significativa cuando se correlacionó la razón de los valores actuales de absorción y deabsorción, a los estadísticamente predecibles por regresión lineal, respectivamente, como función de la razón peso húmedo de la raíz a peso húmedo de la sección vegetativa. Los valores bajos de esta última razón parecen estar asociados con los valores de radiactividad específica mayores que los esperados para ambas fases de absorción y deabsorción. Lo contrario ocurre, generalmente, con respecto a las plántulas con una alta proporción de raíses, con relación a la sección vegetativa.

Bajo las condiciones de razón baja en el peso raíz—sección vegetativa, se sugiere la presencia de un mecanismo activo de translocación y acumulación de minerales en las plantas. Los valores altos de dicha razón darían lugar a un flujo mayormente pasivo, por la vía transpiratoria.

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