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Comparative Investigations on Two Different Types of K/Ca Metabolism: *Kalanchoe* and *Zea**)

By

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With 8 Figures

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Summary

KINZEL H. & BERGER W. 1992. Comparative investigations on two different types of K/Ca metabolism: *Kalanchoe* and *Zea*. – Phyton (Horn, Austria) 31 (2): 307–321, 8 figures. – English with German summary.

Two plant species with different features of mineral metabolism, that is, *Kalanchoe daigremontiana* ("calciotrophic" type) and *Zea mays* (potassium type) were cultivated in nutrient solutions and compared with respect to their different ability to take up and to distribute Ca and K. After some time of development, K in the nutrient solution was replaced by Rb, and the ion shifts within the plants were followed in the light of the changes in contents of the newly absorbed Rb. The K/Ca ratios in the leaves of the plants differed by an order of magnitude, *Kalanchoe* having lower K and higher Ca contents than *Zea*. The added Rb was absorbed by *Kalanchoe* to a much lesser extent than by *Zea,* but transferred into the younger leaves to a higher degree than by *Zea*. The differences between the two species are caused by a more effective Ca uptake system in *Kalanchoe* and a more effective K uptake system in *Zea;* and additonally, as indicated by K and Rb shifts within the plants in the course of the experiment, by differences in the K retranslocation system.

Zusammenfassung

KINZEL H. & BERGER W. 1992. Vergleichende Untersuchungen an zwei verschiedenen K/Ca Stoffwechseltypen: *Kalanchoe* und *Zea*. – Phyton (Horn, Austria) 31 (2): 307–321, 8 Abbildungen. – Englisch mit deutscher Zusammenfassung.

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*) Dedicated to Prof. Dr. Otto HÄRTEL (Graz) on the occasion of his 80th birthday.

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Zwei Pflanzenarten mit verschiedenartigen Typen des Mineralstoffwechsels, nämlich *Kalanchoe daigremontiana* („calciotropher" Typ) und *Zea mays* (Kalium-Typ) wurden in Hydrokultur im Hinblick auf die Aufnahme und Verteilung von Calcium und Kalium verglichen. Nach einiger Zeit der Entwicklung wurde das Kalium in den Nährlösungen durch Rubidium ersetzt, wonach die Ionenverschiebungen in den Pflanzen an Hand der Gehalte an neu aufgenommenem Rubidium verfolgt wurden. Die K/Ca-Quotienten in den Blättern differierten zwischen den beiden Arten um etwa eine Größenordnung, wobei *Kalanchoe* weniger K (bzw. Rb) und mehr Ca enthielt als *Zea*. Das zugefügte Rb wurde von *Kalanchoe* in weit geringerem Maße aufgenommen, jedoch in höherem Maße in die jüngeren Teile transferiert als von *Zea*. Die Unterschiede zwischen den beiden Arten liegen in einem weitaus effektiveren Ca-Aufnahmesystem in *Kalanchoe* und einem effektiveren K-Aufnahmesystem in *Zea*, zusätzlich aber auch, wie aus den Ionenverschiebungen im Zuge des Experimentes hervorgeht, in Unterschieden hinsichtlich des Retranslokationssystems für Kalium.

Introduction

The existence of differences in mineral metabolism between different plant species is well known and relevant both for agronomy and ecology. An early exact experiment on such differences was carried out by COLLANDER 1941 and was recently repeated (PATEL & al. 1980). The culture of different plant species in the identical nutrient solution revealed marked peculiarities with respect to ion uptake. Starting from such basic knowledge, the working group of one of the authors (HK) investigated systematically the distribution of differences ot that kind in the plant kingdom, with emphasis on calcium (HORAK & KINZEL 1971, KINZEL 1984, 1989). It turned out that several clearly distinguishable types of mineral metabolism exist and that often a certain type is more or less related to a certain taxonomic unit (e. g. a genus, a family). For the set of physiological properties that is related to a taxonomic unit, the term "physiotype" has been proposed (ALBERT & KINZEL 1973). Within these taxonspecific types, smaller peculiar differences between species or even genotypic varieties may be found (EPSTEIN & JEFFERIES 1964, BASSAM & al. 1990).

The present paper tries to gain further insights into these relationships for one contrasting pair of plant physiotypes: *Zea mays,* representing the *Poaceae,* and *Kalanchoe daigremontiana,* representing the *Crassulaceae.* The physiotypic qualities of the *Poaceae* include a high K/Ca ratio. HORAK & KINZEL (1971) report K/Ca ratios around 9; according to other authors the ratios may be as high as 30 for *Zea mays* (PATEL & al. 1980) and only exceptionally as low as unity (for *Panicum virgatum* SMITH & GREENFIELD 1979 report a case of an unusually low K content). These data may be interpreted in terms of a very effective system of K absorption in *Poaceae* (KAHN & HANSON 1957, CHINO 1981) and, in the same family, of the ability to restrict the uptake of ions that are abundant in soil, e. g. Ca (KINZEL 1989). The *Crassulaceae,* on the other hand, which were chosen for a contrasting physiotype ("calciotrophic type"), are characterized by a very effective Ca uptake.

As regards Ca uptake, there is a vivid discussion whether it is (or to what degree, resp., it is) a matter of active (metabolic) uptake or mainly a passive intake with the transpiration stream (cf. KINZEL 1989). Indeed, the *Crassulaceae* contain much Ca even if grown in soils poor in Ca (HORAK & KINZEL 1971, ROESSNER & POPP 1989) and, therefore, we may assume that in this family, unlike to many others, active uptake of Ca plays an appreciable role. Additionally, all *Crassulaceae* so far investigated contain no anions which may precipitate Ca, so that nearly all of it is dissolved in the vacuoles of the cells where it may reach a concentration up to 140 mM and a true ionic activity of 50 mM (KINZEL 1989). So, for the characterization of the calciotrophic physiotype, the ratio of dissolved K/dissolved Ca is better suited than the total contents. Ratios around unity or, within the leaves, even appreciably below unity, are characteristic for the calciotrophs.

In consideration of these facts, the question arises what characteristics of ion metabolism cause these differences. The uptake processes in the roots are the ones best investigated (cf. MARSCHNER 1986). However, "the mechanisms which bring about selective ion absorption and transport do not reside only in the roots. Transfer of the ions into the conducting tissues, subsequent movement in the xylem and phloem, absorption by cells in stems and leaves and re-export therefrom – all these and yet other processes are implicated" (EPSTEIN & JEFFERIES 1964). The experimental data available so far, however, are not sufficient for a deeper understanding of the differences in the metabolism that cause the observed differences in the K and Ca contents. We undertook, therefore, a new experimental approach to elucidate these relations.

Materials and methods

Plant culture: Bulbils of *Kalanchoe daigremontiana* R. HAMET & PERR. DE LA BATHIE were laid out on wet quartz sand and frequently sprayed with tap water. After six weeks they were transferred to the substrate. Seeds of *Zea mays* (convar. *amylacea* MONTG., source: Austrosaat, Vienna) were germinated on wet filter paper and transferred after ten days. For growing the plants we used hydroponic pots (10 cm diameter, 500 ml volume for *Kalanchoe,* 15 cm diameter, 600 ml volume for *Zea*) filled with perlite (pre-washed with diluted HCl and rinsed with deionized water).

The basic nutrient solutions: It turned out to be impossible to cultivate the two species in the identical nutrient solutions because of their different demands particularly for K and Fe. The nutrient solutions were prepared as follows:

Kalanchoe solution after ROESSNER 1986, solution 4

KNO_3	1.5 mM
$Ca(NO_3)_2$	0.75 mM
$MgSO_4$	0.4 mM
$MnCl_2$	3.6 µM
$ZnSO_4$	0.3 µM
Fe-EDTA	3.6 µM
H_3BO_3	7.2 µM

Phosphorus demand was met by adding a buffer solution, mixed from 8 ml 0.2 M $(NH_4)_2HPO_4$ and 92 ml 0.2 M $(NH_4)H_2PO_4$ and adjusted to pH 6. Of this buffer, 8 ml were added to 1 liter of nutrient solution so that the phosphate content amounted to 1.6 mM and the content of NH_4^+ 1.7 mM.

Zea solution, modified after CHIZZOLA 1985:

KNO_3	4.5 mM
$Ca(NO_3)_2$	0.25 mM
$MgSO_4$	1.0 mM
$(NH_4)_2HPO_4$	0.1 mM
NH_4NO_3	1.0 mM
$MnCl_2$	6.0 µM
$ZnSO_4$	3.0 µM
Fe-EDTA	6.0 µM
H_3BO_3	7.2 µM
$CuSO_4$	2.0 µM

The pots were placed in a greenhouse with normal daylight, temperature 24–27° C by day, 20–21° C by night, air humidity about 60%. The nutrient solutions were changed every 7 days for *Kalanchoe* and, because of marked acidification, every 3 days for *Zea*.

The principle of the experiment: ROESSNER 1986 concluded from his observations that in the leaves of *Kalanchoe* (and, presumably, of other members of the *Crassulaceae* too) the low K/Ca ratio may be caused not only (or not even primarily) by an intense Ca absorption. Roots, stems and the xylem sap in his experiments contained more K than Ca even in plants in which the leaves contained appreciably more Ca than K. In *Kalanchoe* leaves the K content exceeded the Ca content only if the plants were cultivated in nutrient solutions with high K content. In solutions with moderate K content, however, K/Ca ratios in the leaves below unity were typical, and even lower ratios were observed in Crassulacean plants from the natural vegetation (ROESSNER & POPP 1986). ROESSNER assumed that part of the K, which at first has been transported into the leaves, is then re-exported and redistributed within the plant. In order the test this assumption, we used Rb, which is well-known to be handled by the same ion uptake and transport systems as K. We did not, however, use the radioactive isotope ^{86}Rb which is widely used in ion uptake experiments, but non-radioactive Rb. The intention of our work was, indeed, to follow quantitatively the ion shifts that take place after having replaced the K in the nutrient solution by Rb, in the light of the time course of K and Rb contents in the respective organs. Of course, Rb cannot fully replace K in its physiological functions (MARSCHNER 1986), so that alterations in the metabolism of organic substances may take place in plants supplied with Rb instead of K (COHEN & al. 1978, CUSIDÓ & al. 1987). In the ion transport processes in a strict sense, however, Rb behaves rather similar to K (Fig. 7–11 in EPSTEIN 1972, DIAZ DE LA GUARDIA & al. 1985, BERGBACK & BORG 1989). Only in K-starved plants the behaviour of Rb seems to be more complicated (BENLLOCH & al. 1989).

Handling of samples: After sufficient development of the plants (*Kalanchoe* produced 6 tiers of leaves within 9 weeks, *Zea* 8 tiers of leaves within 4 weeks) the pots were arranged in six groups of three pots for *Kalanchoe* and in five groups for *Zea*. One group served as the control; in all others, after rinsing with deionized water, the former nutrient solutions were replaced by other ones which contained Rb instead of K. The plants were harvested, from a group of three pots at a time, 12, 36, 82, 180 and 372 hours after Rb addition for *Kalanchoe*, and 24, 74, 146 and 242 hours after Rb addition for *Zea*. The plants were partitioned into the leaf fractions, (separately for every tier of every plant), stems and roots, placed in paperbags and ovendried at 50° C. With the *Kalanchoe* leaves, it was necessary to let them lie at room temperature for one week before oven-drying, to avoid the emergence of sap from the succulent leaves. The whole of every fraction was cut in pieces, extracted with 1 M HCl (1 hour at 95° C) and the extract made up to volume. In the extracts, Ca and K were determined by atomic absorption photometry, and Rb by flame emission photometry (Perkin-Elmer 3030). The data represent the arithmetic means of the respective fractions of the three plants of every group (that is, of every time of harvesting). Only in one case (Fig. 8), all of the three numbers are shown to give an impression of the variability.

Results and discussion

The overall contents of K and Ca: Analysis of the control group (the zero hour group, prior to the Rb addition) revealed the great differences between the two species investigated. Fig. 1 reflects the K/Ca ratios in leaves of different age. It was necessary to use a logarithmic scale to show the differences which, in some cases, amount to more than one order of magnitude. In general, the quotients rise with rising leaf number and indicate that Ca accumulates in the oldest leaves whereas the younger leaves contain more K. This is in accordance with many previous results (cf.

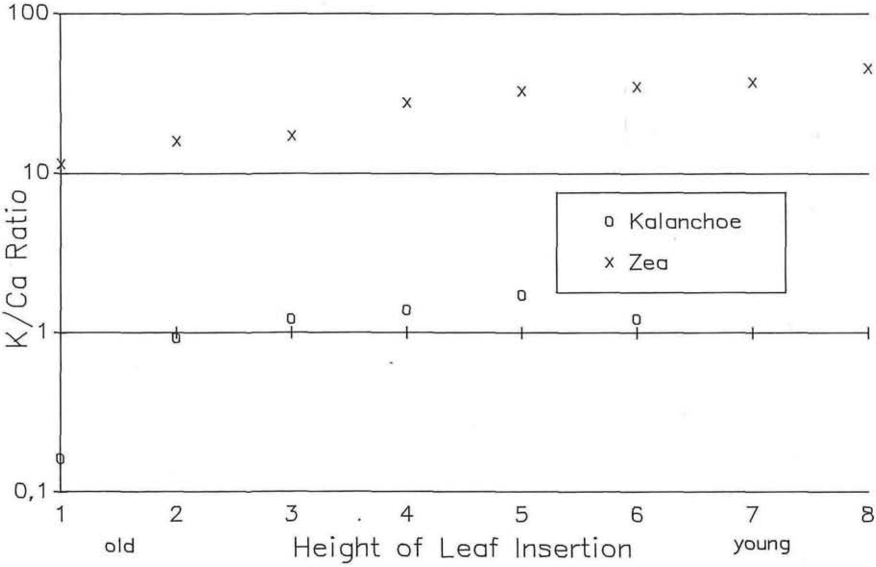

Fig. 1. Molar Ca/K ratios in *Kalanchoe* and *Zea* leaves of decreasing age.

KINZEL 1989) and supports the opinion that Ca moves mainly in the xylem with the transpiration stream. In the discussion on this subject, several experimental results are mentioned which seem to indicate that the transpiration has no effect on ion uptake (recently, for example, TANNER & BEEVERS 1990 for maize). Results of this kind depend, however, on the plant and ion species under investigation, and the ion concentration in the nutrient solution or in the soil. *Poaceae* (like Maize) tend to restrict passive intake, and therefore the high active uptake of K and the low active uptake of Ca determine the composition of the plant organs (for reviews, see ALBERT 1982 and KINZEL 1982). Indeed, even in *Poaceae* the contribution of passive intake of Ca with the transpiration stream can come into evidence if only the concentration in the nutrient solution is high enough: Fig. 4.15 in KINZEL (1982) shows – after experiments of LAZAROFF & PITMAN – that in barley the effect of the transpiration is visible only if the Ca concentration in the nutrient solution is 15 mM, not, however in 0.5 mM. The Ca concentration in the experiments of TANNER & BEEVERS (1990) was 2 mM! In many other plant species the contribution of passive Ca intake with the transpiration stream is more prominent. A leaf, therefore, tends to contain the more Ca the more water it has transpired during its lifetime, whereas the phloem-mobile K is transported to the young growing organs. It should be noted, however, that differences in Ca metabolism between "physiotypes" may be even more marked if related not to the total Ca content, but to the fraction of water-soluble Ca. *Chenopodiaceae,* for example, may contain much Ca, but only as insoluble Ca oxalate because in this family a tendency prevails to synthesize enough oxalate to precipitate all incoming Ca (STEINER & KINZEL 1980, LECHNER 1989). *Crassulaceae,* on the other hand, are characterized not only by taking up much Ca but also by containing most of it in a water-soluble form (HORAK & KINZEL 1971, ROESSNER & POPP 1986).

The question arises whether the differences in K and Ca contents may be caused only by the different composition of the nutrient solutions: the *Kalanchoe* solution contains three times as much Ca as the *Zea* solution, but only one third as much K. In Tab. 1, the ratios in Ca contents in leaves (*Kalanchoe*/*Zea*) are set against the respective ratios in the nutrient solutions. *Kalanchoe* leaves contain 20 times as much Ca as *Zea* leaves, whereas the *Kalanchoe* solution contains only three times as much. On the other hand, Tab. 2 reveals that the K contents generally reflect the composition of the nutrient solutions. Another difference between the nutrient solutions regards the N contents: The *Zea* solution contains twice as much NO_3^- than the *Kalanchoe* solution, whereas the NH_4^+ contents are of the same order of magnitude. It is well known that NO_3^- increases the cation uptake. So, one could speculate about an influence of the NO_3^- contents on the high K uptake in *Zea*. If this effect would dominate the results, however, Ca uptake should likewise be increased in *Zea,* which is not the case. Furthermore, differences of this kind between *Poaceae* and *Crassulaceae* have been found

Table 1

Ratio between Ca in *Kalanchoe* leaves/Ca in *Zea* leaves, and between Ca levels in the respective nutrient solutions.

Time	youngest leaves	oldest leaves	nutrient solutions
Zero hour	22.2	19.6	3
End of experiment	20.7	18.3	

Table 2

Ratio between K in *Kalanchoe* leaves/K in *Zea* leaves, and between K levels in the respective nutrient solutions.

Time	youngest leaves	oldest leaves	nutrient solutions
Zero hour	0.5	0.28	0.3
End of experiment	0.6	0.3	

also in plants of the natural vegetation (HORAK & KINZEL 1971), so that there is scarcely any doubt of the "physiotypical" character of the differences.

The reported results lead to the assumption that *Kalanchoe* (and probably other *Crassulaceae* too) grows best with a relatively high concentration of Ca in its substrate and is endowed with a very effective Ca uptake system. However, species belonging to the *Crassulaceae* may be adapted even to soils poor in Ca, but in this situation also the ample capacity of their Ca uptake system results in a relatively high Ca content (HORAK & KINZEL 1971), as is peculiar to the "calciotrophs". *Zea,* on the other hand, is more demanding with respect to K, N and Fe.

Unfortunately, the available information about Ca intake into plants is rather poor. The interest of recent investigators focusses on the processes that pump Ca out of the cytoplasm, either through the cellular membrane, the plasmalemma (RASI-CALDOGNO & al. 1990), through "microsomal" (= ER) membranes (WILLIAMS & al. 1990) or through the vacuolar membrane, the tonoplast (SCHUMAKER & SZE 1990). The active Ca uptake processes in the roots, which seem to be rather low, have been scarcely investigated in recent times (cf. the very short chapter on this subject in MARSCHNER 1983, p. 23). Indeed, differences in the efficiency of Ca uptake have been reported (MARSCHNER 1986, p. 497), but, as in the present paper, only in terms of Ca contents, not by characterising the ion uptake systems in the roots. In the very efficient Ca accumulators like *Crassulaceae,* the well-known passive uptake through the transpiration stream may be supplemented by an active component which would be more prominent than in the bulk of the plant species.

Table 3

Ca and K contents in leaves of *Kalanchoe daigremontiana.*

Leaf	Harvest time, hours after addition of Rb						
number	0	12	36	82	180	372	0
	Ca mmoles/g DM						K mmoles/g DM
1 (old)	2.55	1.88	2.14	2.07	1.57	1.22	0.41
2	0.87	0.97	1.02	1.01	0.79	0.72	0.81
3	0.74	0.61	0.72	0.63	0.69	0.56	0.91
4	0.65	0.56	0.59	0.47	0.52	0.49	0.92
5	0.54	0.52	0.54	0.46	0.44	0.43	0.94
6 (young)	0.66	0.67	0.6	0.52	0.61	0.35	0.81

The peculiar behaviour of the oldest leaves of *Kalanchoe:* Table 3 shows the Ca and K contents of *Kalanchoe* leaves of different ages. All harvest times are included for Ca, but only time 0 (prior to Rb addition) for K, because later on the K contents are influenced by the intake of Rb. The oldest leaves have double the amount of Ca and half the amount of K as compared to all younger leaves. At every harvest time a new group of three plants was analyzed, and all of them showed this behaviour; thus the results cannot be accidental. All other leaves show the slope of composition which is common in plants: with decreasing age the Ca contents fall and the K contents gradually rise (except, in this case, the youngest leaves). Of course, this means no real export of Ca from leaves. Actually, the young leaves have less water transpired during their lifetime and therefore accumulated less Ca than the older ones. The peculiar behaviour of the respective oldest leaves (highly increased Ca content) seems to be a characteristic of *Kalanchoe,* and perhaps of *Crassulaceae* in general.

Differences in Rubidium uptake and distribution: The capacity for uptake of Rb (as a model for K) is much greater in *Zea* than in *Kalanchoe,* as may be seen in the oldest leaves (Fig. 2), and very similar, only at an elevated general level, in the younger ones. The Rb contents increase up to 241 μmol/g dry matter in the oldest and up to 512 μmol/g DM in the youngest leaves of *Zea*, compared with 25.5 and 138 μmol/g DM, respectively, in *Kalanchoe.* As is well known, the monovalent alkali ions are transferred in both species mainly into the young leaves. If one calculates the ratio in Rb contents of young versus old leaves (Fig. 3), a further feature is seen. Because of the above mentioned peculiar behaviour of the oldest leaves in *Kalanchoe,* the values from the second oldest leaves versus youn-

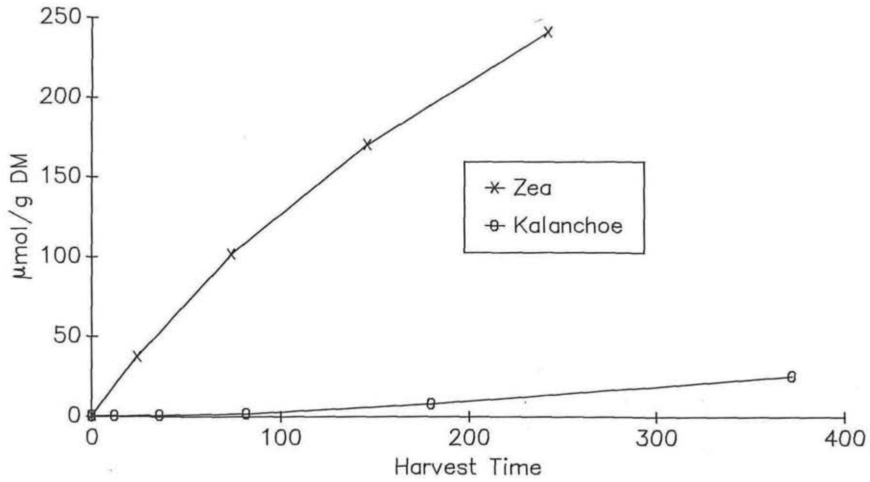

Fig. 2. Rubidium contents in the oldest leaves of *Kalanchoe* and *Zea* at different times (hours) after replacing K in the nutrient solutions by Rb.

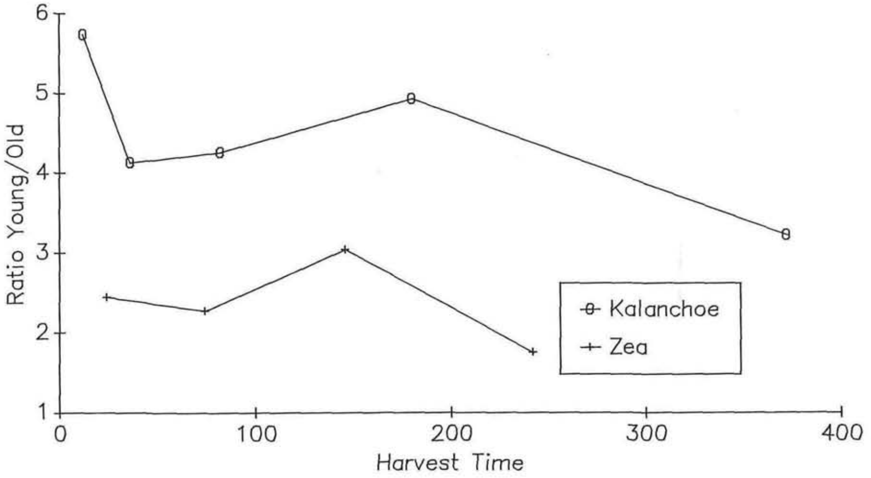

Fig. 3. Rubidium contents in *Kalanchoe* and *Zea:* Quotients youngest/second oldest leaves at different times (hours) after replacing K in the nutrient solutions by Rb.

gest leaves are shown. In absolute figures, *Kalanchoe* takes up less Rb than *Zea*, but transfers this little Rb at an even higher proportion into the young leaves than *Zea*.

The fate of K taken up prior to Rb addition: A reasonable assumption would be that the freshly absorbed Rb gradually dilutes the K that was already in the leaves at the beginning of the experiment. This was

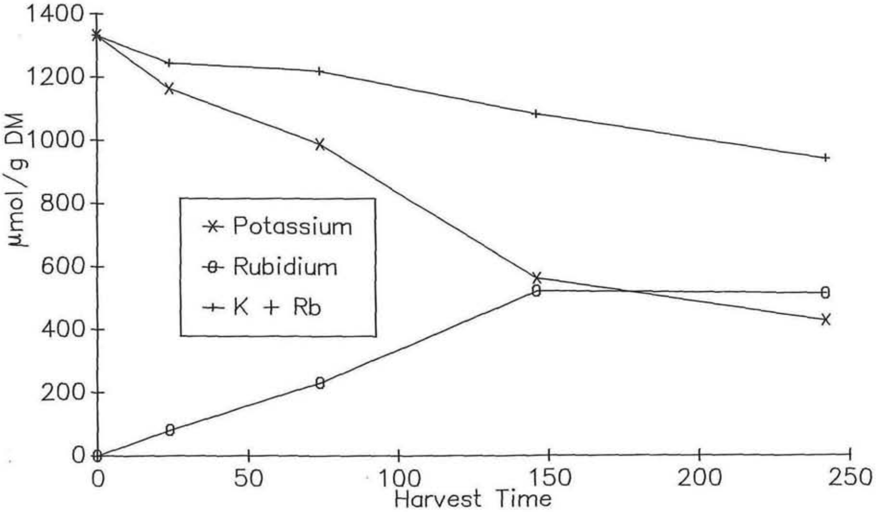

Fig. 4. K and Rb contents and sum of K + Rb in the youngest leaves of *Zea* at different times (hours) after replacing K in the nutrient solutions by Rb.

the case, for example, in the youngest leaves of *Zea* (Fig. 4). At the end of the experiment, the Rb contents exceeded the K contents. The sum of K and Rb decreased a little as compared with the initial state. The older leaves of *Zea* behave quite similarly, with the difference that the Rb contents do not reach such high values and amount to only a small fraction of the (K + Rb) sum. In the youngest leaves of *Kalanchoe* the Rb contents are much lower than the K contents, and the sum (K + Rb) decreases more than in *Zea*. The oldest leaves of *Kalanchoe*, however, differ not only in the K contents at zero hour (as is shown in Tab. 3); the K contents also exhibit a peculiar course during the experiment (Fig. 5): a rapid fall until hour 36 and a gradual increase thereafter.

An even better insight into the ion shifts is offered by diagrams that show the K contents of all leaves at all harvest times (Fig. 6 and 7). Viewing these two figures, one should have in mind that they show only the changes in the K contents without an insight into the changes in Rb, which take place simultaneously. With *Zea* (Fig. 7), in all but the two oldest leaves the K contents markedly fell from the beginning of the experiment, in the course of being replaced by Rb. Only in the two oldest leaves it rose from hour zero to hour 24. With *Kalanchoe,* on the contrary, an initial rise occurred in all leaves but the oldest one, from hour zero to hour 24 or 36 (only in the leaf pair 5, K seemed to be – in the mains – fairly constant until hour 36). In the oldest leaves of *Kalanchoe,* however, the K contents were much lower than in the other leaves; they fell until hour 36 and then gradually rose to a value somewhat higher than the initial one (Fig. 6).

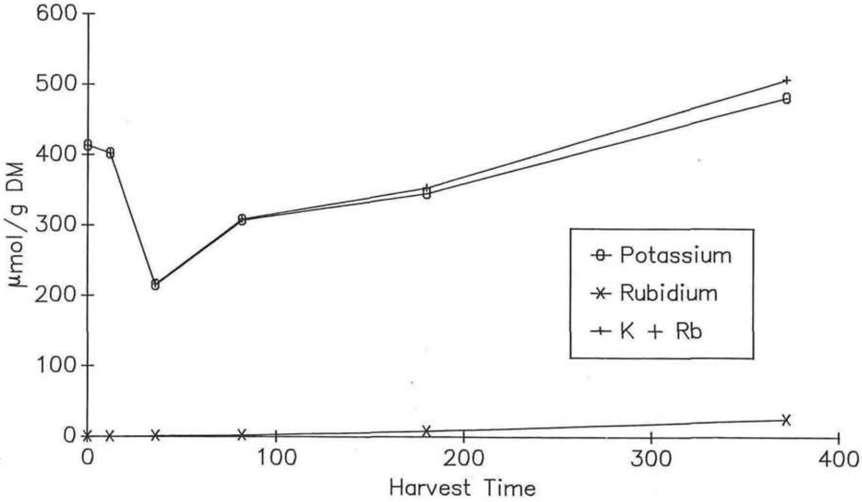

Fig. 5. K and Rb contents and sum of K + Rb in the oldest leaves of *Kalanchoe* at different times (hours) after replacing K in the nutrient solutions by Rb.

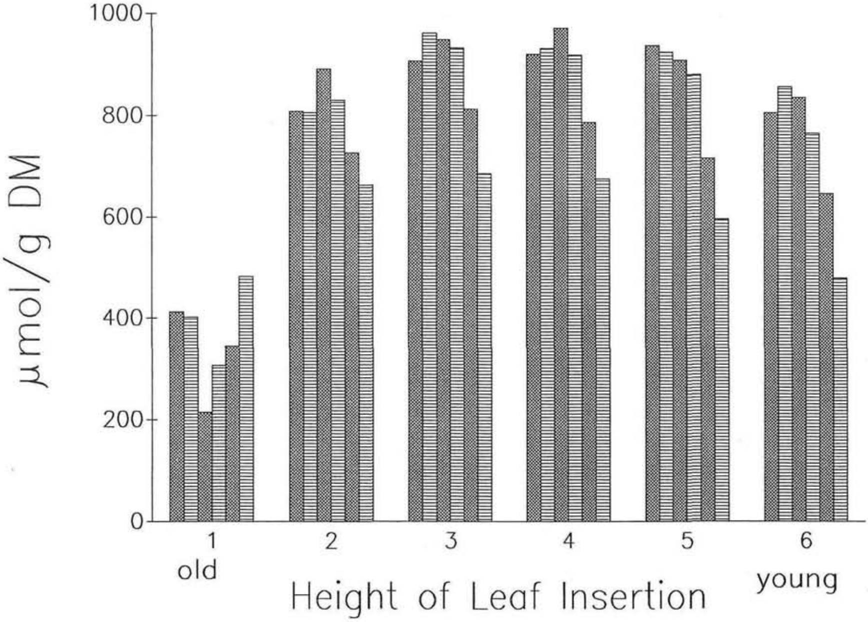

Fig. 6. K contents in *Kalanchoe* leaves. The groups of bars correspond to the leaf numbers (heights of insertion). Within every group, the single bars are arranged according to the time course after replacing K in the nutrient solutions by Rb (from left to right: 0, 12, 36, 82, 180, 372 hours).

Attempting to interpret these processes, one could assume that the newly absorbed univalent cations are mainly shifted in the acropetal direction (at different rates in the two species, cf. Fig. 3) and transferred, after some time (seemingly 36 hours, under these conditions), into another pool from which they are recirculated in the basipetal direction; and this to a much greater extent in *Kalanchoe* than in *Zea*. Whether this change may be related to a cellular pool (cytosol, ER, vacuoles) or to a tissue pool (leaf parenchyma, xylem or phloem parenchyma or the phloem itself) cannot be decided on the basis of the present results. The offered explanation in general, however, is supported by the initial decrease of K in the oldest leaves of *Kalanchoe*, compared with a tendency to an initial increase in the younger leaves. The general decrease in the younger leaves of *Kalanchoe* and *Zea* is assumed to be due mostly to the dilution by Rb, but at least in *Kalanchoe* may be caused in part by a recirculation into the oldest leaves, the K contents of which rose from hour 36 on.

In order to test this hypothesis in the light of additional observations, in Fig. 8 the respective K and Rb contents in the roots of *Kalanchoe* are presented. In this figure, the values of K contents of every individual plant are shown, to visualize their variability, and additionally the arithmetic means of Rb contents in the course of the experiment. Roots behave like the oldest leaves, in that the K contents fell up to hour 36 and began to rise

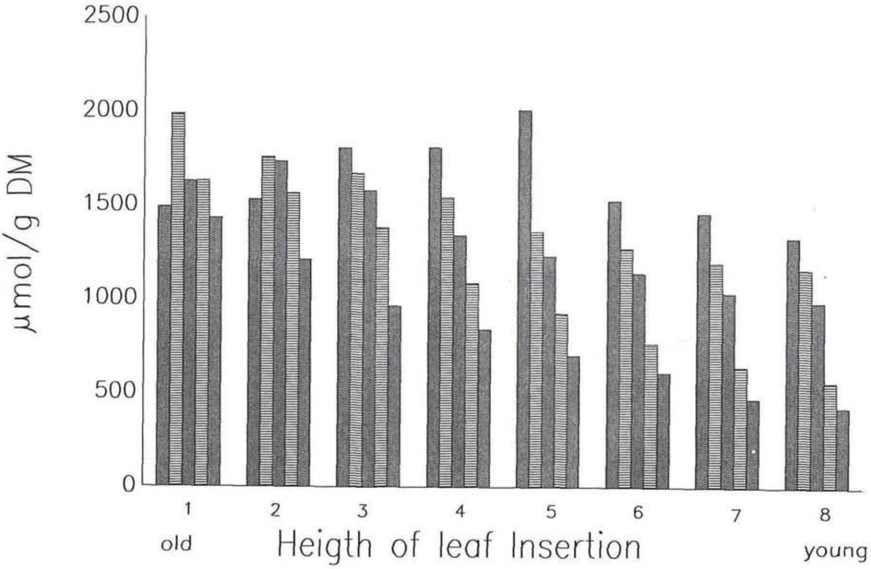

Fig. 7. K contents in *Zea* leaves. Similar to Fig. 7; the groups refer to the eight investigated developmental stages of leaves. The single bars of every group correspond (from left to right) to hours 0, 24, 74, 146, 242 from the start of the experiment (replacement of K by Rb).

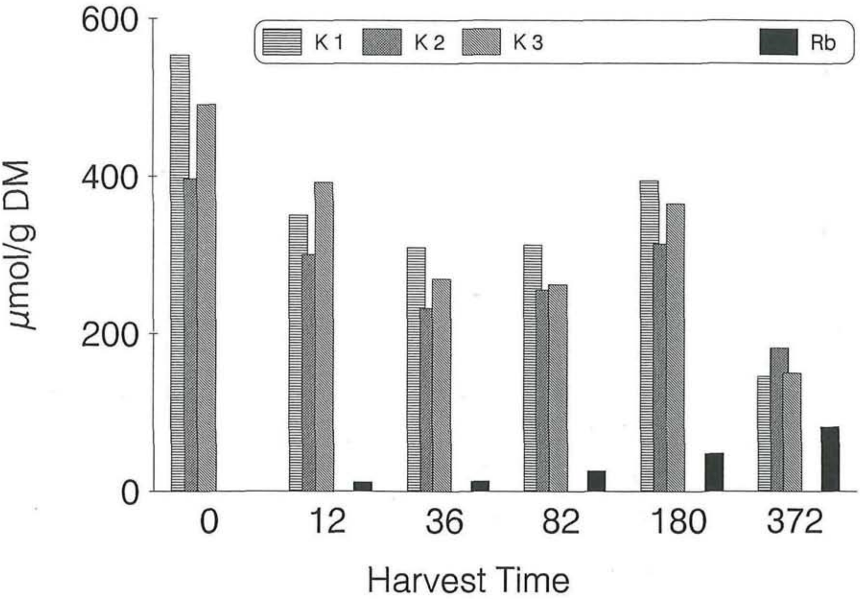

Fig. 8. K and Rb contents in roots of *Kalanchoe* at different times (hours) after replacing K in the nutrient solutions by Rb. At every time, the three overlapping bars refer to the three single determinations of K (diverging from the other figures, where the means of the three parallel determinations are given). The smaller single (black) bars right of the triple group correspond to the respective Rb contents.

thereafter. The Rb contents in the *Kalanchoe* roots are surprisingly low, considering that they are in direct contact with the Rb-containing nutrient solution. Between hour 180 and 372, a rapid fall of K contents takes place, concomitantly with a rise of Rb to about half the amount of K. These observations may indicate that the recirculation of K – after the initial period of 36 hours – proceeds downwards into the roots. The eventual rapid fall in K contents may indicate one of two events – or both of them simultaneously: Perhaps an excretion of K into the nutrient solution begins at that time which provides the capacity for raising the Rb contents – or at that time the Rb/K rate in the younger parts of the plant has reached a degree which causes the Rb to be introduced into the recirculation process.

Though the character of the "calciotrophic" physiotype is fully pronounced only in the leaves (the stems often contain more K than Ca: Roessner 1986), our results lead to the conclusion that the differences in mineral composition between *Zea* and *Kalanchoe* are caused mainly by differences in the uptake systems for K and Ca and, additionally, in the K retranslocation system. Differences with the latter system reported in the literature range from 20% K retranslocation in tomato (ARMSTRONG & KIRKBY 1979) to an entire lacking of a K retranslocation system in *Striga hermonthica* (SMITH & STEWART 1990).

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