Calcium (^{45}Ca) Mobility in Chicory Root (*Cichorium intybus* L.) as Affected by the Anionic Composition of the Nutrient Solution during Forcing

Karine Fouldrin and Anis Limami¹

Fédération Nationale des Producteurs d'Endive, Institut National de la Recherche Agronomique, Laboratoire du Metabolisme et de la Nutrition des Plantes, Route de Saint-Cyr, 78026 Versailles Cedex, France

Thierry Lamaze

Institut National de la Recherche Agronomique, Laboratoire de Biochimie et Physiologie Végétales (Centre National de la Recherche Scientifique-Unité de Recherche Associée 573), 34060 Montpellier, France

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Abstract. During forcing, the witloof chicory taproot produces an etiolated bud, the chicon. The axis of this organ often is brown as a consequence of a disorder associated with a localized Ca deficiency. The effect of the main anions (NO_3^- , Cl^- , SO_4^{2-}) in the nutrient solution on Ca (^{45}Ca) absorption and translocation in the chicon was investigated. Although the amount of Ca that accumulated in the chicon was not affected by nutrient solution composition, Ca (^{45}Ca) mobility was modified. The amount of radioactivity in the chicon increased slightly when the main anion in the solution was sulfate and decreased markedly when the main anion was chloride, compared to nitrate. Calculations of the specific radioactivity of Ca reaching the chicon and in root tissue suggest that, when slowed down, Ca transport consists of a homogeneous flow in all root tissues, whereas, in other cases, Ca moves along a preferential pathway, such as the xylem vessels. Modifying the anionic composition of the nutrient solution to avoid a localized Ca deficiency is discussed.

The chicon is an etiolated bud produced by forcing the tuberized root of witloof chicory plants in darkness. The axis of the chicon often is brown with cavities, a characteristic that greatly diminishes crop quality. Electron microscopic studies of these cavities reveal that this disorder is caused by tissue necrosis due to the breakdown of cell wall and plasma membranes (Den Outer, 1989). The disorder is similar to apple (*Malus domestica* Borkh) bitter pit, tomato (*Lycopersicon esculentum* Mill.) blossom-end rot, lettuce (*Lactuca sativa* L.) tip burn, and potato (*Solanum tuberosum* L.) brown spot (Bangerth, 1979; Poovaiah, 1986) and is associated with a localized Ca^{2+} deficiency.

Because of the ability of Ca^{2+} to form inter- and intra-molecular coordination complexes in the apoplasm (Wuytack and Gillet, 1978) and low Ca^{2+} concentrations in the cytosol and phloem sap, Ca^{2+} is considered the most immobile cation in the plant (Mengel and Kirkby, 1987). Therefore, the Ca^{2+} requirement of enlarging organs cannot be met by the xylem or phloem supply, even when large amounts of this ion are supplied to the plant (Kirkby, 1979; Wiersum, 1979). The Ca^{2+} ion moves upward in xylem vessels mainly via the transpiration stream or root pressure when transpiration is reduced (Palzkil and Tibbitts, 1977). However, this transport does not depend only on water flow, since exchange with the apoplastic negatively charged molecular groups also is involved (Clarkson, 1984). In fact, the xylem cylinder acts as an exchange column, and chelated Ca^{2+} is more readily translocated than free Ca^{2+} (Ferguson and Bollard, 1976; Van de Geijn and Petit, 1979). This result suggests that Ca^{2+} nutrition could be affected greatly by other cations due to competition for negative sites in the

walls. Indeed, previous absorption of Ca^{2+} or other cations such as K^+ , a process that results in the saturation of the apoplastic electronegative complex, increased Ca^{2+} transport (Singh and Jacobson, 1979). When the N source is ammonium, disorders linked to Ca^{2+} deficiency are more likely than when the N source is nitrate (Kirkby, 1979).

Studies of Ca^{2+} movement have paid little attention to the effect of counter-anions in the nutrient solution on Ca^{2+} uptake and transport by the plant. According to Wiersum (1979), the presence of chloride in addition to nitrate in the nutrient medium enhanced Ca^{2+} uptake and transport to the leaves in *Ricinus communis* L. Nevertheless, the influence of the valence or mobility of the main anion in the outer medium has been neglected.

This article is concerned with Ca (^{45}Ca) absorption and transport in witloof chicory taproots when the main anion in the hydroponic culture medium was no longer the usual mobile inorganic anion nitrate, but chloride, another mobile anion, or sulfate, a rather immobile one.

Materials and Methods

Plant material. 'Flash' witloof chicory seeds were sown in a field in northern France at the end of April. At the beginning of November, the aerial parts of the plants were excised and roots were harvested. The tips of the latter were cut off so that all roots were 15 cm long. Roots were stored for 4 months at 0°C before being forced.

Forcing conditions. Roots were forced in a dark chamber at 18°C and 90% relative humidity (RH). The temperature was maintained constant via a system (Realis, Villejuif, France) that controls the temperature to within 0.5°C of that desired. RH was less well regulated and depended on a humidifier. We estimate, however, that the maximum variation was $\approx 5\%$. During this period, roots were placed in plastic buckets filled with 4 cm of an aerated nutrient solution. Thus, only the lower part of the root was immersed in the nutrient solution (100 ml/plant). The nutrient

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¹To whom reprint requests should be addressed.

Fig. 1. Diagram of the test system. Chicory plants were placed in plastic buckets standing in 4 cm of an aerated nutrient solution.

solution was renewed twice per 24 h. (Fig. 1).

Nutrient solutions. In the nutrient solution normally used for forcing chicory, the principal anion is NO_3^- (Lesaint and Coïc, 1983). To assess the effect of other anions on Ca^{2+} transport, 16-day forced plants were supplied for 5 days, from day 16 to 21 of forcing, with nutrient solutions in which 10.9 mM NO_3^- was replaced by 10.9 mM chloride (Table 1) or 5.45 mM sulfate. Control plants were maintained on NO_3^- solution. The nutrient solutions were labeled with ^{45}Ca (830 kBq·mmol $^{-1}$) during the 5 days of treatment.

Assays. After 2 or 5 days (day 18 or 21 of forcing), six plants from each treatment were harvested. The roots were washed three times in 100 ml demineralized water for 1 min each time and dried on filter paper. The adventitious roots were removed, since they contributed only a negligible amount of dry matter and Ca^{2+} or ^{45}Ca content compared to the taproot (data not shown). The chicon was separated from its root, and the latter was divided into four parts:

lower (4 cm), middle-a, middle-b, and upper; these parts corresponded to the remainder of the root divided into three equal parts (Fig. 1). The chicon and root parts were weighed, freeze-dried, ground, and homogenized.

Cations were extracted for 12 h from 2-g samples of the dried tissue with 50 ml 0.1 N HCl. Calcium and Mg were assayed in the extraction medium by an atomic absorption spectrophotometer (model IL151; Instrumentation Laboratory, Lexington, UK), and potassium was assayed by an emission spectrophotometer (Eppendorf, Hamburg, Germany). Radioactivity was determined by liquid scintillation using 0.5 ml extraction medium/4.5 ml cocktail scintillator after quenching compensation. The results represent the amount of exogenous Ca (^{45}Ca) calculated as the ratio of the label in the tissue and the specific radioactivity of the medium (kBq·mg $^{-1}$ dry weight/kBq· μmol^{-1} Ca^{2+}).

Anions were extracted from a 100-mg aliquot of dried tissue with 15 ml demineralized water at 100°C for 1 h. Nitrate, chloride, sulfate, and phosphate were assayed using an ion-exchange chromatograph and conductivity detector (model 4000i; high-performance liquid chromatography AS4A column, Dionex Corp., Sunnyvale, Calif.).

The cation exchange capacity (CEC) of the root was estimated according to a modified version of the method used by Wacquant (1974). Subsamples (3 g) of freeze-dried powder were soaked for 10 min in 150 ml 0.05 N HCl, 0.025 M $\text{Ca}(\text{NO}_3)_2$ at pH 6.5, and 0.05 N HCl. Between each treatment, the sample was recovered by centrifugation (15 min, 10000× g) and washed twice in demineralized water for 1 min each time. Values corresponded to the amount of Ca ion present in the last medium.

Data analysis. The average specific radioactivity for each root part (Sm) during the 5 days of the labeling was estimated by the mean of the specific radioactivities before (S_1) and after (S_2) treatment [$\text{Sm} = (S_1 + S_2) / 2$]. Since before treatment there is no radioactivity in the tissue, S_1 is nil; thus, $\text{Sm} = S_2 / 2$.

For each root part, Sm was compared to the specific radioactivity of the Ca^{2+} flux reaching the upper parts of the plant (Sf) during

Table 1. Composition of nutrient solutions. Plants were supplied with an NO_3^- solution during the first 16 days of forcing, then with an NO_3^- , a Cl-NO_3^- , or an $\text{SO}_4\text{-NO}_3^-$ solution until day 21. Nutrient solutions were labeled with ^{45}Ca .

Ions	Ion concn (mM)		
	Nutrient solution		
	NO_3^-	Cl-NO_3^-	$\text{SO}_4\text{-NO}_3^-$
NO_3^-	20.80	9.90	9.90
PO_4^{3-}	1.65	1.65	1.65
Cl^-	0.00	10.90	0.00
SO_4^{2-}	0.00	0.00	5.45
K^+	8.40	8.40	8.40
Ca^{2+}	4.20	4.20	4.20
Mg^{2+}	1.25	1.25	1.25
NH_4^+	3.30	3.30	3.30

labeling. Therefore, $Sf = Q^{45}\text{Ca}/Q\text{Ca}$, where $Q^{45}\text{Ca}$ is the radioactivity accumulated in the tissues above the given part and $Q\text{Ca}$ is the quantity of Ca accumulated in these tissues during treatment. Values were expressed as the mean of six replications $\pm$ SE. The experiment was duplicated and similar data were obtained. The data shown are those for one experiment.

Results

At the end of the experiment, the loss of dry matter by the roots and the accumulation of dry matter by the chicons were similar for plants supplied with NO_3^- , Cl^- , or SO_4^{2-} as the main anion in the nutrient solution (Table 2). Determining the amount of NO_3^- , Cl^- , SO_4^{2-} , and inorganic phosphate (P_i) in the tissues (root and chicon) gave similar results for the various treatments. The exception was that

Table 2. Chicory root and chicon biomass changes during forcing.

Forcing (days)	Biomass ² (g dry wt/organ)					
	Nutrient solution					
	NO_3		Cl-NO_3		$\text{SO}_4\text{-NO}_3$	
	Root	Chicon	Root	Chicon	Root	Chicon
16	16.93 (2.17)	6.51 (0.42)	16.93 (2.17)	6.51 (0.42)	16.93 (2.17)	6.51 (0.42)
18	17.62 (4.65)	7.35 (0.61)	18.97 (5.54)	4.46 (1.23)	19.92 (3.16)	4.30 (0.85)
21	16.32 (1.99)	8.09 (0.51)	18.33 (3.85)	7.78 (0.80)	17.27 (4.17)	8.40 (0.82)

²Values are the mean of six replications ($\pm$ SE).

the amount of a given anion (NO_3^- , Cl^- , or SO_4^{2-}) per plant was slightly higher when the anion in question was the main anion in the nutrient solution (Table 3). Concentrations of K^+ , Mg^{2+} , and Ca^{2+} in the root and chicon did not differ among treatments (Table 4).

As already reported by Limami and Lamaze (1991), when NO_3^- was the main anion in the medium, the total amount of Ca^{2+} in the root remained almost constant, while the rate of Ca^{2+} transport to the chicon increased during chicon development. Our results (Table 4) show that this was true when the plants were supplied with $\text{SO}_4\text{-NO}_3$, or Cl-NO_3 solutions. The quantity of Ca^{2+} that accumulated in the chicons was similar for all plants with all nutrient solutions used. However, compared to plants supplied with NO_3 solution, the rates of ^{45}Ca uptake and translocation to the upper part of the plant, and especially the chicon, were depressed for plants supplied with Cl-NO_3 solution (Fig. 2). In contrast, radioactivity in the upper tissues increased slightly in all plants supplied with $\text{SO}_4\text{-NO}_3$ solution. This result clearly indicates that, even though the anionic composition of the nutrient solution did not affect the rate of net Ca uptake and its subsequent exportation to the chicon, it altered the characteristics of Ca^{2+} movement in the plant (Fig. 2).

In chicory, Ca^{2+} migration to the chicon involves transport along xylem vessels in addition to an exchange process with Ca^{2+} ions in the surrounding tissues (Limami and Lamaze, 1991). To estimate if the effects on ^{45}Ca movement were related to changes in the Ca^{2+} transport process through the root, S_m was compared to S_f during the 5 days of labeling. The mean value of S_f was about twice (S_m/S_f is ≈ 0.5) that of S_m when plants were supplied with NO_3 or $\text{SO}_4\text{-NO}_3$ solutions (Table 5). S_f and S_m were similar (S_m/S_f is ≈ 1) when plants were supplied with Cl-NO_3 solution.

Table 3. Concentrations of anions [Cl^- , SO_4^{2-} , inorganic P (P_i), and NO_3^-] in the chicory root and chicon during forcing.

Anion	Forcing (days)	Anion concn ² (mmol/organ)					
		Nutrient solution					
		NO_3		Cl-NO_3		$\text{SO}_4\text{-NO}_3$	
		Root	Chicon	Root	Chicon	Root	Chicon
Cl^-	16	2.06 (0.30)	1.03 (0.10)	2.06 (0.30)	1.03 (0.10)	2.06 (0.30)	1.03 (0.10)
	18	2.04 (0.32)	1.34 (0.16)	2.11 (0.13)	1.04 (0.37)	2.38 (0.27)	0.96 (0.12)
	21	1.74 (0.35)	1.39 (0.17)	2.33 (0.33)	1.37 (0.13)	2.04 (0.60)	1.37 (0.25)
	16	1.52 (0.08)	0.72 (0.01)	1.52 (0.08)	0.72 (0.01)	1.52 (0.08)	0.72 (0.01)
	18	1.95 (0.16)	0.99 (0.09)	1.85 (0.14)	0.42 (0.14)	1.92 (0.13)	0.37 (0.14)
	21	1.48 (0.28)	1.10 (0.15)	1.52 (0.46)	0.92 (0.13)	1.89 (0.45)	1.19 (0.15)
SO_4^{2-}	16	0.50 (0.05)	0.80 (0.19)	0.50 (0.05)	0.80 (0.19)	0.50 (0.05)	0.80 (0.19)
	18	0.52 (0.27)	1.02 (0.12)	0.48 (0.15)	0.63 (0.31)	0.43 (0.14)	0.63 (0.09)
	21	0.45 (0.09)	1.41 (0.11)	0.41 (0.17)	1.27 (0.15)	0.43 (0.15)	1.33 (0.21)
	16	0.33 (0.06)	0.12 (0.03)	0.33 (0.06)	0.12 (0.03)	0.33 (0.06)	0.12 (0.03)
	18	0.35 (0.12)	0.22 (0.07)	0.26 (0.05)	0.03 (0.02)	0.17 (0.11)	0.02 (0.01)
	21	0.39 (0.15)	0.34 (0.05)	0.16 (0.04)	0.19 (0.08)	0.24 (0.10)	0.23 (0.09)

²Values are the mean of six replications ($\pm$ SE).

Table 4. Concentrations of cations (Ca^{2+} , Mg^{2+} , and K^+) in the chicory root and chicon during forcing.

Cation	Forcing (days)	Cation concn ^z (mmol/organ)					
		Nutrient solution					
		NO_3		Cl-NO_3		$\text{SO}_4\text{-NO}_3$	
		Root	Chicon	Root	Chicon	Root	Chicon
Ca^{2+}	16	1.62 (0.16)	0.48 (0.13)	1.62 (0.16)	0.48 (0.13)	1.62 (0.16)	0.48 (0.13)
	18	1.68 (0.23)	0.71 (0.19)	1.81 (0.35)	0.60 (0.35)	1.69 (0.26)	0.61 (0.07)
	21	1.68 (0.24)	0.93 (0.19)	1.60 (0.16)	0.79 (0.17)	1.69 (0.32)	0.87 (0.06)
Mg^{2+}	16	0.78 (0.12)	0.54 (0.03)	0.78 (0.12)	0.54 (0.03)	0.78 (0.12)	0.54 (0.03)
	18	0.73 (0.16)	0.54 (0.09)	0.68 (0.14)	0.43 (0.14)	0.70 (0.13)	0.47 (0.14)
	21	0.62 (0.07)	0.65 (0.04)	0.64 (0.16)	0.72 (0.10)	0.69 (0.11)	0.78 (0.15)
K^+	16	10.55 (1.53)	4.87 (0.44)	10.55 (1.53)	4.87 (0.44)	10.55 (1.53)	4.87 (0.44)
	18	10.31 (1.81)	5.67 (0.38)	10.79 (2.07)	4.50 (1.61)	11.25 (1.64)	4.03 (0.61)
	21	8.85 (1.23)	6.75 (0.24)	9.35 (2.59)	6.79 (0.82)	10.83 (2.25)	7.74 (0.75)

^zValues are the mean of six replications ($\pm$ SE).

Tissue CEC, on which Ca^{2+} movement is supposed to depend partly (Clarkson, 1984; Ferguson and Bollard, 1976), was measured in roots of plants supplied with the various nutrient solutions. This characteristic (expressed on a whole-root basis) was not influenced by the anionic composition of the nutrient solution and remained nearly constant during treatment (Table 6).

Discussion

Most variables investigated; i.e., changes in root and chicon dry matter, tissue ion composition, inorganic anion-cation balance, and CEC, were not affected by lowering the NO_3^- concentration in favor of Cl^- or SO_4^{2-} in the nutrient solution. The main features of Ca^{2+} transport during forcing; i.e., acceleration of net Ca^{2+} absorption by the root and of subsequent Ca^{2+} translocation and accumulation in the chicon, were not modified by changing the main anion (NO_3^- , Cl^- , or SO_4^{2-}) in the nutrient solution. Ca^{2+} delivery to the chicon may be related to the neutralization of negative charges appearing in the new tissues of the growing chicon, as suggested for meristems by Van De Geijn and Smeulders (1981). That SO_4^{2-} , NO_3^- , and Cl^- solutions did not affect biomass production by the chicon, or probably the number of negative charges in this organ, may explain why these solutions did not affect net Ca^{2+} transport.

However, an important modification appeared concerning ^{45}Ca accumulation in the root and chicon when the plants were supplied with Cl-NO_3 solution. The radioactivity in the upper part of plants supplied with Cl-NO_3 solution was lower than in plants supplied with NO_3 and $\text{SO}_4\text{-NO}_3$ solutions. Since total Ca^{2+} absorption and accumulation were not altered in plants supplied with Cl-NO_3 solution, Cl^- , therefore, decreased Ca^{2+} mobility in the tissues. Changes in Ca^{2+} mobility were associated with simultaneous changes in Ca transport, as suggested by comparing ^{45}Ca Sm and Sf. If the transport occurred exclusively along a preferential pathway, such as the xylem vessels, without exchange occurring with surrounding tissues (Limami and Lamaze, 1991), Sf should

be higher than Sm, since there is no isotopic dilution of the upward-moving ^{45}Ca with the stable isotope of the tissues surrounding the vessels. Conversely, if the upward migration of Ca^{2+} involved a complete and immediate exchange of newly supplied ^{45}Ca with the Ca pools of various tissues, without any preferential pathway, Sm and Sf would be similar.

The hypothesis that Ca^{2+} travels along a preferential pathway was supported, since Sf was twice Sm when NO_3^- or SO_4^{2-} was the main nutrient solution anion. However, as reported for NO_3^- , the difference is too small to disregard the fact that Ca^{2+} translocation involved long-distance transport in the xylem and exchange with Ca^{2+} ions in the surrounding tissues. In plants supplied with Cl-NO_3 , Sf was similar to Sm, so the depressive effect of Cl^- on Ca^{2+} mobility in the plant seemed to be associated with a concomitant increase in the exchange of transported Ca^{2+} with Ca^{2+} in tissues adjacent to the preferential pathway.

Chloride, like NO_3^- , is a monovalent anion that is readily absorbed, transported, and accumulated to high levels in plant tissues. In contrast, SO_4^{2-} is a slowly absorbed divalent anion. Surprisingly, in the presence of SO_4^{2-} and NO_3^- , Ca^{2+} transport was similar to that in the presence of NO_3^- alone, whereas the presence of Cl^- depressed Ca^{2+} mobility. That both NO_3^- and SO_4^{2-} , unlike Cl^- , are assimilable ionic species must not be disregarded. Our results did not agree with those of Wiersum (1979), who showed that Ca^{2+} net uptake and transport to the leaves of *R. communis* increased when part of CaNO_3 in the nutrient solution was substituted by CaCl . One important difference between their experimental methods and ours was that the *Ricinus* plants were cultivated in a glasshouse and likely transpired freely during the day. In contrast, the *Cichorium* plants were forced under high RH in the dark and transpired little. Therefore, in *Ricinus* plants, Ca^{2+} transport to the leaves was associated, in part, with transpiration, whereas in *Cichorium* plants, Ca^{2+} transport to the chicon was accompanied by low water flux originating from root pressure or was due to the development of the chicon, which acted as a sink. This result suggests that the effects of Cl^- on Ca^{2+} transport may depend on the

Fig. 2. Calcium accumulation in the chicon and in four parts of the chicory root when supplied with solutions of NO_3 (Δ), Cl-NO_3 ($\bullet$), or $\text{SO}_4\text{-NO}_3$ ($\square$) labeled with ^{45}Ca . Means of six replications; bars represent $\pm\text{SE}$.

Table 5. Comparison of the ^{45}Ca specific radioactivity of each root part (Sm) with that of the Ca flux reaching the upper parts of the plant (Sf).

Root part	Radioactivity ($\text{Q}^{45}\text{Ca}/\text{QCa}$)		
	Nutrient solution		
	NO_3	Cl-NO_3	$\text{SO}_4\text{-NO}_3$
Upper			
Sm	0.04	0.02	0.05
Sf	0.05	0.02	0.08
Sm/Sf	0.80	1.00	0.63
Middle b			
Sm	0.07	0.04	0.09
Sf	0.14	0.05	0.18
Sm/Sf	0.50	0.80	0.50
Middle a			
Sm	0.10	0.09	0.14
Sf	0.29	0.15	0.33
Sm/Sf	0.34	0.60	0.42
Lower			
Sm	0.22	0.26	0.29
Sf	0.53	0.35	0.67
Sm/Sf	0.42	0.74	0.43

Table 6. Cation exchange capacity (CEC) of the chicory root.

Forcing (days)	CEC ^z (meq/root dry wt)		
	Nutrient solution		
	NO_3	Cl-NO_3	$\text{SO}_4\text{-NO}_3$
0	2.37 (0.08)	2.37 (0.08)	2.37 (0.08)
16	2.02 (0.36)	2.02 (0.36)	2.02 (0.36)
18	2.74 (0.29)	1.95 (0.50)	2.63 (0.31)
21	2.89 (0.58)	2.51 (0.06)	2.12 (0.10)

^zValues are the mean of three replications ($\pm\text{SE}$).

magnitude of water flux through the plant.

Incipient stages of browning occur during the first days of forcing (data not published). At this time, the chicon is a minute bud and Ca fluxes are low, a condition that renders any study of Ca^{2+} transport to this organ difficult. During this period, organic matter flux from the root to the bud, an action that permits chicon growth, may be much higher than Ca^{2+} flux, a result that leads to Ca^{2+} deficiency in the newly formed tissue. As the growth of the chicon progressed, the rate of Ca^{2+} transport to the chicon increased (Limami and Lamaze, 1991) and no more browning occurred in the chicon. This pattern agrees with the observation of Shear (1975) that the N-Ca ratio in the leaves and fruit of 'York Imperial' apples was related more closely to the incidence of bitter pit than was Ca^{2+} level alone.

Our results show that modifying the anionic composition of the nutrient solution did not induce changes in Ca^{2+} supply to the growing chicon, but affected Ca^{2+} mobility in the plant. No significant difference was observed in Sm and Sf (i.e., during Ca transport) between plants supplied with $\text{SO}_4\text{-NO}_3$ solution and those supplied with NO_3 solution, while the stimulating effects of SO_4^{2-} on Ca^{2+} mobility, although small, were significant. This difference may have resulted from the fact that any change in

radioisotope accumulation was detected more easily than a change in Sf and Sm. Thus, modifying the anionic composition of the nutrient solution by increasing the concentration of SO_4^{2-} at the beginning of forcing may be a good strategy to avoid a localized Ca^{2+} deficiency that could lead to browning of the chicon axis.

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