Planta (1989) 177:237–244

Planta

Sucrose uptake and partitioning in discs derived from source versus sink potato tubers

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Abstract. The uptake of sucrose into isolated discs cut from sink (growing) and source (sprouting) potato (*Solanum tuberosum* L.) tuber tissue was studied. The uptake of sucrose into sink-tuber discs demonstrated biphasic kinetics. The large saturable component was inhibited by incubation of the discs with *p*-chloromercuribenzene sulfonic acid (PCMBS) whilst both the saturable and linear components were inhibited by carbonyl cyanide *m*-chlorophenylhydrazone (CCCP). By contrast, in source-tuber discs, the linear component represented the majority of sucrose taken up, the saturable component playing only a minor role. In source discs, only the saturable component of uptake was inhibited by either PCMBS or CCCP. A large proportion (up to 25%) of sucrose taken up into sink-tuber discs was converted to starch but as the tubers aged the proportion of sucrose converted to starch decreased to the level found in source-tuber discs (approx. 3%). By contrast with sink-tuber discs (see Oparka and Wright, 1988b, Planta **175**, 520–526) sucrose uptake into source discs was insensitive to turgor and demonstrated an uptake pattern similar to that of CCCP-treated sink tissue. It is proposed that exogenous sucrose is taken into the storage parenchyma of sink-tuber discs by both a carrier-mediated and a diffusional process. By contrast, uptake into the storage parenchyma of source-tuber discs appears to be essentially diffusional. The turgor sensitivity of sucrose uptake into sink-tissue discs may be mediated via the plasmalemma H^+-ATPase. As the tuber ages the sucrose-uptake activity decreases and the capacity of the storage parenchyma to synthesise starch is lost. The data are discussed in relation to the in-vivo mechanisms of sucrose transport in storage tissues.

Key words: Apoplast – Metabolic inhibitors – Partitioning (sucrose) – *Solanum* (source, sink tubers) – Sucrose uptake

Introduction

Sucrose transport in source leaves has been the subject of intensive investigation in recent years. The apoplastic concept of phloem loading (for a review, see Giaquinta 1983) has recently been challenged (Van Bel 1987) although there is still much evidence presented in its support (Delrot 1987). The unloading of sucrose from the phloem apparently occurs by a variety of mechanisms depending on the organ involved (for a review see Thorne 1985). In potato tubers, previous studies investigating the mechanism of unloading have demonstrated the presence of numerous plasmodesmata connecting the phloem with surrounding storage cells (Oparka 1986) indicating the potential for symplastic transport of sucrose into the storage parenchyma. Furthermore, studies involving the efflux of [^{14}C]sucrose into solute-collecting wells indicate that at least part of the transport pathway from the phloem is via the symplast (Oparka and Prior 1987). By contrast, studies with discs isolated from growing tubers have shown that uptake of exogenous sucrose seems to occur via an active, carrier-mediated transport mechanism and that both uptake and partitioning of sucrose to starch are sensitive to turgor (Oparka and Wright 1988a, b).

One of the major disadvantages in attempting to study loading and unloading within a single plant is that the sources and sinks are often both

spatially separated and anatomically different, making the mechanisms involved in loading and unloading extremely difficult to compare. The sink-source transition which occurs in dicotyledonous leaves has provided an opportunity to study sucrose transport within a single organ. This approach has been used to demonstrate the presence of a symplastic unloading pathway in developing leaves of sugar-beet (Schmalstig and Geiger, 1985) and to investigate the mechanisms involved in the sink-to-source transition in tobacco leaves (Fellows and Geiger 1974; Turgeon 1984). However, the latter investigations do not rule out the possibility that different regions of phloem are involved in the unloading and loading of sucrose.

In contrast to the developing leaf, in which sucrose is utilised for growth, the growing potato tuber represents a massive storage sink for assimilates in which starch is the major reserve. At the end of a growing season, when the stolon connection to the parent plant is severed, the tuber undergoes a period of dormancy. Sprouting then occurs, accompanied by mobilisation of storage reserves from the perimedulla (Davies and Ross 1984). Anatomical evidence indicates that starch mobilisation occurs initially around the existing internal phloem strands of the perimedulla (Ross and Davies 1985), the same tissue in which unloading predominated in the growing tuber (Oparka and Prior 1987). The tuber thus undergoes a sink-to-source transition with little apparent change in internal anatomy.

To date, changes in sucrose-uptake characteristics during the sink-to-source transition occurring in vegetative storage organs appear not to have been studied. This feature has therefore been utilised in the present study to compare the uptake and partitioning of sucrose in isolated discs cut from the perimedulla of both growing (sink) and sprouting (source) tubers.

Material and methods

Plant material

Sink potato tuber tissue. Potato (*Solanum tuberosum* L. cv. Record) plants were grown from seed tubers (40–45 mm diameter) in square ($20 \cdot 20\ cm^2$) pots containing compost. Glasshouse temperatures were maintained at 20° C during the day and 15° C at night. Daughter potato tubers were harvested from the plants after they had reached a diameter of at least 3 cm. Growing potato tubers represent strong sinks for assimilates, which are unloaded mainly from the central perimedulla region of the tuber (Ahmed and Sagar 1981; Oparka and Prior 1987).

Source potato tuber tissue. Seed-potato tubers (cv. Record, 40–45 mm) were planted in compost and maintained at 15° C in the dark. The parent tubers were used for sucrose-uptake experiments when the sprouts arising from them were at least 2 cm in length. Such sprouting tubers have been demonstrated to be rapidly mobilising storage carbohydrates, initially from areas around the internal phloem groups (Davies and Ross 1984; Ross and Davies 1985).

Field-grown tubers. In order to examine progressive changes in sucrose uptake during tuber growth, seed-potato tubers were planted in the field on April 27th, 1987 and used in sucrose-uptake experiments at two-week intervals between 16th July and 30th September. At each harvest the daughter tubers growing on three replicate plants were removed and discs cut from the perimedulla of four tubers on each plant. The tubers were selected so that the average tuber weight per plant was represented at each harvest date. The discs were selected at random for use.

Experimental procedures

The procedures for washing discs, pretreatment with the inhibitors *p*-chloromercuribenzene sulfonic acid (PCMBS) and carbonyl cyanide *m*-chlorophenylhydrazone (CCCP), equilibration in different mannitol concentrations and uptake of [^{14}C]sucrose were the same as described previously (Oparka and Wright 1988a, b). Following washing, the discs were preincubated with inhibitor or appropriate osmoticum before transfer to a second solution containing unlabelled sucrose and [U-^{14}C]sucrose 9.25 $kBq \cdot ml^{-1}$ (specific activity 20 $GBq \cdot mmol^{-1}$; Amersham International, Amersham, Bucks, UK). After incubation for 3 h the discs were washed for 3×3 min in the appropriate osmoticum, minus sucrose and inhibitors, to remove free-space sucrose. They were then extracted twice in 80% ethanol at 70° C for a total of 6 h. Radioactivity in the ethanol-soluble fraction was determined by scintillation counting and the discs were combusted on a sample oxidiser (Packard 306) for determination of total insoluble ^{14}C. This insoluble component contains over 90% starch (Oparka and Wright 1988b) and in all experiments reported here is designated the starch fraction.

Results

Time course of sucrose uptake. The total uptake of sucrose into discs of both sink and source potato tubers increased linearly with time between 0.5 and 10 h, discs from sink tubers taking up more sucrose than those from source tubers (Fig. 1). The linear regression of sucrose uptake with time intercepted the y axis at a positive value, approx. 14 µl of apoplastic [^{14}C]sucrose being trapped in the free-space after the wash-out period. The wash-out procedure was therefore standardised at 3×3 min, in which time the majority (>70%) of the free-space sucrose was removed from the discs. This ensured that the error produced by retention of free-space sucrose was at least identical in all treatments, except under conditions which caused plasmolysis (see also Oparka and Wright 1988b).

The amount of sucrose converted to starch in both sink and source tubers was also linear with respect to time, intercepting the origin. Thus, the rate of diffusion of sucrose from the apoplast into

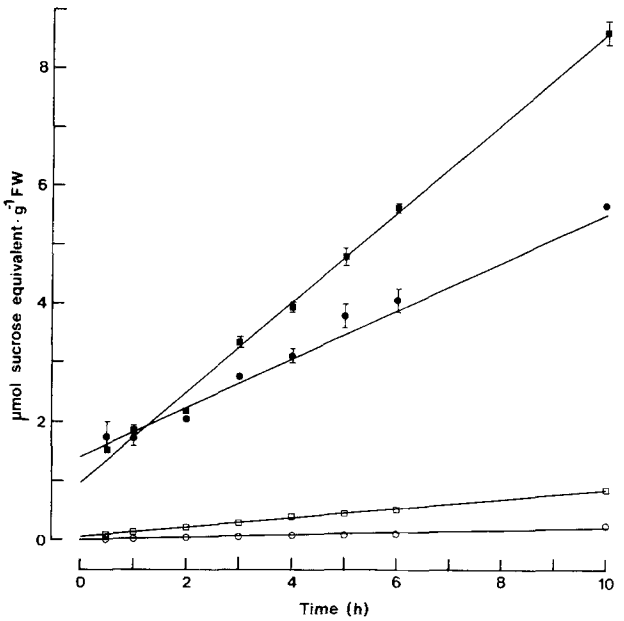

Fig. 1. Time course of total sucrose uptake (*closed symbols*) and the amount of sucrose converted to starch (*open symbols*) by discs of source and sink potato tubers. Incubation media contained 50 mM sucrose, 250 mM mannitol, 25 mM 2-(N-morpholino)ethanesulfonic acid (Mes) pH 6.5 and 9.25 kBq ml^{-1} ^{14}C sucrose. ■, sink total uptake ($y=764\ x+987.3$, $r=0.998$); ●, source total uptake ($y=415.7\ x+1406.6$, $r=0.995$); □, sink starch ($y=79.34\ x+71.43$, $r=0.998$); ○, source starch ($y=22.97\ x+-2.98$, $r=0.974$)

the cells did not limit starch synthesis (compare Gifford and Bremner 1981).

Following the initial time-course experiments, discs were routinely incubated with radiolabel for 3 h.

Sucrose uptake versus sucrose concentration. The total uptake of sucrose into sink-tuber discs, from solutions adjusted to 300 mM osmoticum, demonstrated biphasic kinetics (Fig. 2a), apparent saturation kinetics being observed as the exogenous concentration was raised. These were superimposed on a non-saturable, presumably diffusional component as demonstrated by an Eadie-Hofstee transformation of the uptake data (Fig. 2a, insert). Treatment with PCMBS inhibited the total uptake of sucrose into sink tissue, inducing linear kinetics, although the slope of the linear component of sucrose uptake was the same as under control conditions. By contrast, sucrose uptake in the presence of CCCP was linear and greatly reduced in comparison with both control and PCMBS-treated tissues (Fig. 2a).

The total uptake of sucrose into source-tuber discs was reduced in comparison with sink tissue but remained biphasic. However, in marked contrast to sink tissues, neither PCMBS nor CCCP greatly reduced sucrose uptake relative to untreated tissue discs, both inhibitors inducing linear kinetics, demonstrating that the component with saturation kinetics was relatively small. The amount of sucrose taken up into untreated source-tuber discs was approximately equal to that in PCMBS-treated sink discs (compare Fig. 2b with 2a).

Sucrose-to-starch conversion. In sink discs the amount of sucrose converted to starch was strongly biphasic with respect to external sucrose concentration but linear in the presence of both PCMBS and CCCP (Fig. 3a), the latter reducing starch synthesis to a level approx. 20% of that in control discs.

In source discs the conversion of sucrose to starch was also biphasic with respect to external sucrose concentration (Fig. 3b), the biphasic nature of the conversion being confirmed by an Eadie-Hofstee plot (Fig. 3b, insert). However, starch synthesis in source-tuber discs was greatly reduced in comparison with sink tissues. Interestingly, the amount of starch synthesised by untreated source-tissue discs was practically similar to that in CCCP-treated sink-tissue discs (compare Fig. 3a and 3b).

Treatment with PCMBS reduced conversion of sucrose to starch in source discs by eliminating the saturable component. However, in contrast with sink tissue, CCCP did not significantly reduce sucrose-to-starch conversion further than the PCMBS-treated source tissue.

Turgor sensitivity of sucrose uptake. In sink potato tuber tissues both the uptake and conversion of sucrose to starch are optimised at low but positive cell turgors (Oparka and Wright 1988b). At a turgor pressure of 80 kPa uptake was optimised in both control and PCMBS-treated discs. Increased uptake from mannitol solutions above 400 mM was shown to be the result of plasmolysis, allowing increased retention of [^{14}C]sucrose in the free-space. In that investigation of sink tissue, treatment with PCMBS reduced sucrose uptake but did not alter the relationship between uptake and external mannitol concentration, a turgor response still being evident. However, uptake in the presence of CCCP increased as the mannitol concentration increased but did not show an optimum at 300 mM external mannitol. For convenience, these relationships in sink discs are summarised in Fig. 4a.

In marked contrast, sucrose uptake into untreated source tissue did not show the same turgor response as sink tissue discs when incubated in so-

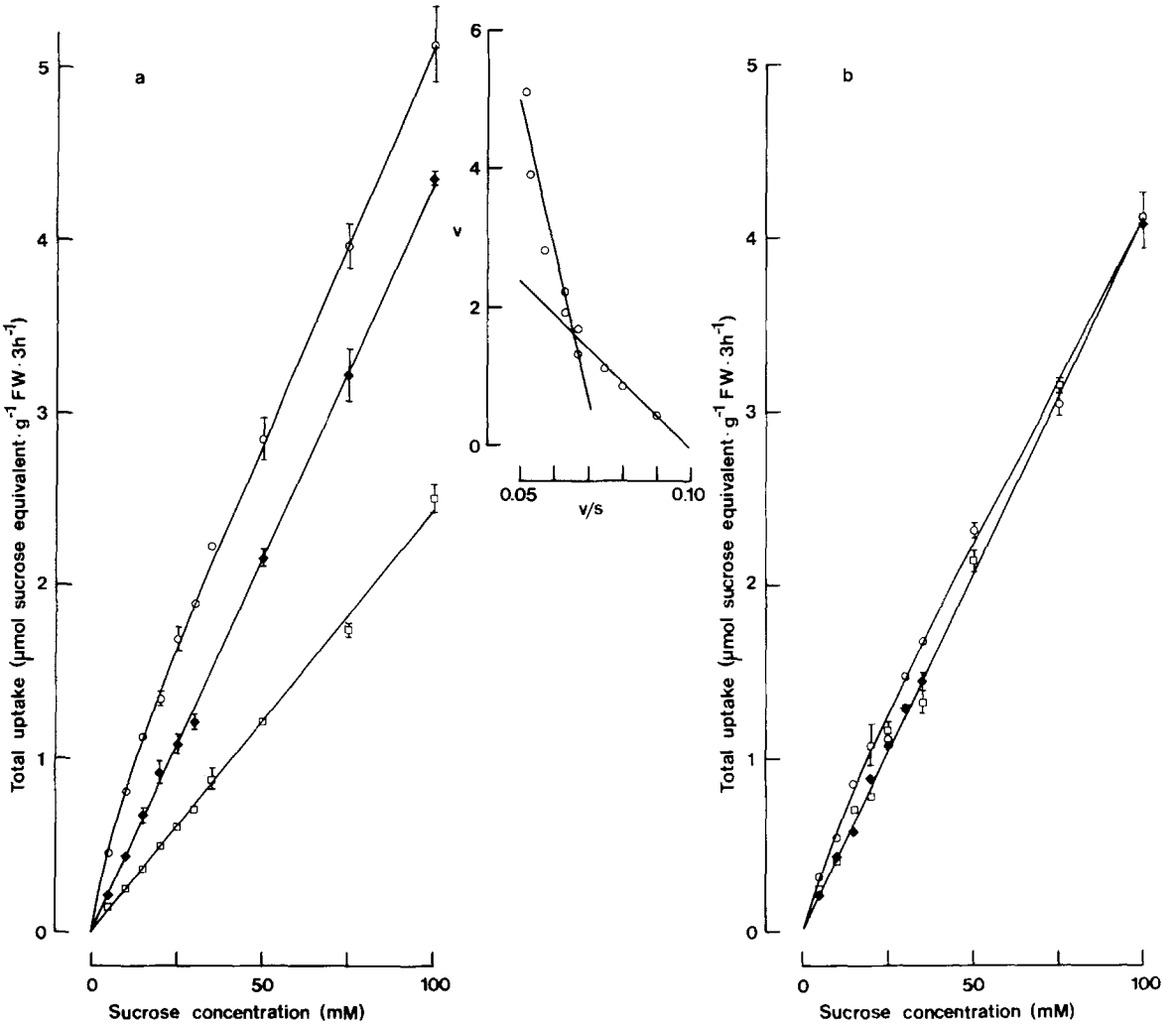

Fig. 2a, b. Total sucrose uptake into discs of **a** sink and **b** source potato tubers from a solution adjusted to 300 mM total osmoticum without inhibitors (○) or in the presence of PCMBS (◆) or CCCP (□). **a** *Insert:* an Eadie-Hofstee transformation of the total uptake data from sink discs incubated without inhibitors. Lines were fitted by eye

lutions containing increasing concentrations of mannitol (Fig. 4b). Instead, uptake into source discs showed an identical pattern to that obtained in sink tissues treated with CCCP (compare Fig. 4b with 4a), uptake increasing continuously as the mannitol concentration increased. Furthermore, inclusion of PCMBS and CCCP resulted in a slight reduction in sucrose uptake with respect to control source tissues but did not alter the shape of the relationship between uptake and external mannitol concentration. The nature of the effect of mannitol concentration on sucrose uptake in the presence of CCCP has yet to be determined although it may be caused by changes in membrane permeability or may reflect the isotopic equilibrium between the radiolabel and endogenous sucrose levels in response to the osmotic environment.

Sucrose uptake during tuber growth. The uptake of sucrose into discs cut from field-grown tubers was investigated at two-week intervals throughout a growing season (Fig. 5). Whilst the total amount of sucrose taken up decreased as the season progressed, the amount of ^{14}C remaining as sucrose, expressed as a percentage of the total label incorporated into the discs, increased from 74% in rapidly bulking tubers to 96% following shoot senescence.

Discussion

The present investigation has highlighted the physiological differences between potato tuber storage parenchyma when it is acting as a sink tissue and when acting as a source.

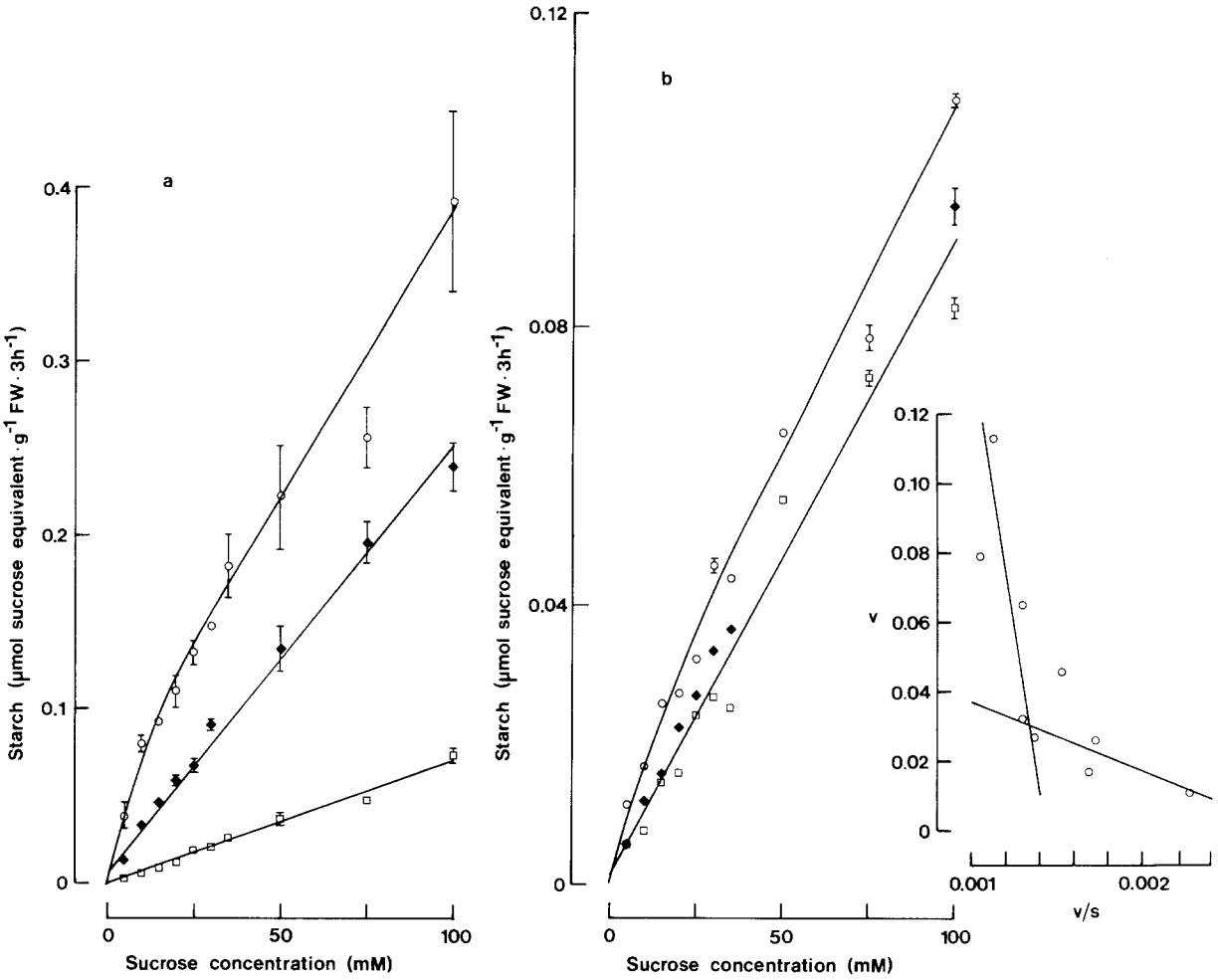

Fig. 3a, b. The amount of sucrose converted to starch in discs of **a** sink and **b** source potato tubers incubated in the same treatments as in Fig. 2. **b** *Insert*: an Eadie-Hofstee transformation of the amount of starch formed in source tubers in the absence of inhibitors

Sucrose uptake versus sucrose concentration. Sucrose uptake and conversion were remarkably different in source versus sink tubers. In sink tubers, sucrose uptake was inhibited strongly by both PCMBS and CCCP. The saturable component of uptake (see also Thorne 1982) was eliminated by PCMBS but the slope of the linear component was not altered. It is likely that the saturable component represented carrier-mediated uptake (see Delrot 1987). The sensitivity of the saturable component to CCCP supports the hypothesis that the carrier for sucrose requires energy, presumably via its coupling to the plasmalemma H^+-ATPase. Biphasic sucrose-uptake kinetics have been reported for a number of source (Maynard and Lucas 1982) and sink (Thorne 1982; Saftner et al. 1983) tissue types, although interpretations differ concerning the nature of uptake. The biphasic uptake of sucrose into isolated protoplasts of soybean cotyledons has been interpreted to represent simultaneous carrier-mediated proton/sucrose symport and passive diffusion across the plasmalemma (Lin et al. 1984; Schmitt et al. 1984). However Daie (1987a) has demonstrated that isolated phloem strands of celery take up sucrose by a single saturating component, whilst uptake into the storage parenchyma cells exhibit only linear kinetics. Biphasic uptake was only observed when the tissue contained a mixture of phloem and storage tissues indicating that the two components of sucrose uptake in this system were spatially separated.

In the sink-potato discs used in the present study the amount of sucrose converted to starch was strongly biphasic. Although sieve elements may contain small quantities of starch, the conversion of unloaded sucrose to starch occurs predominantly in the large storage-parenchyma cells of the perimedulla. The observed biphasic sucrose-uptake

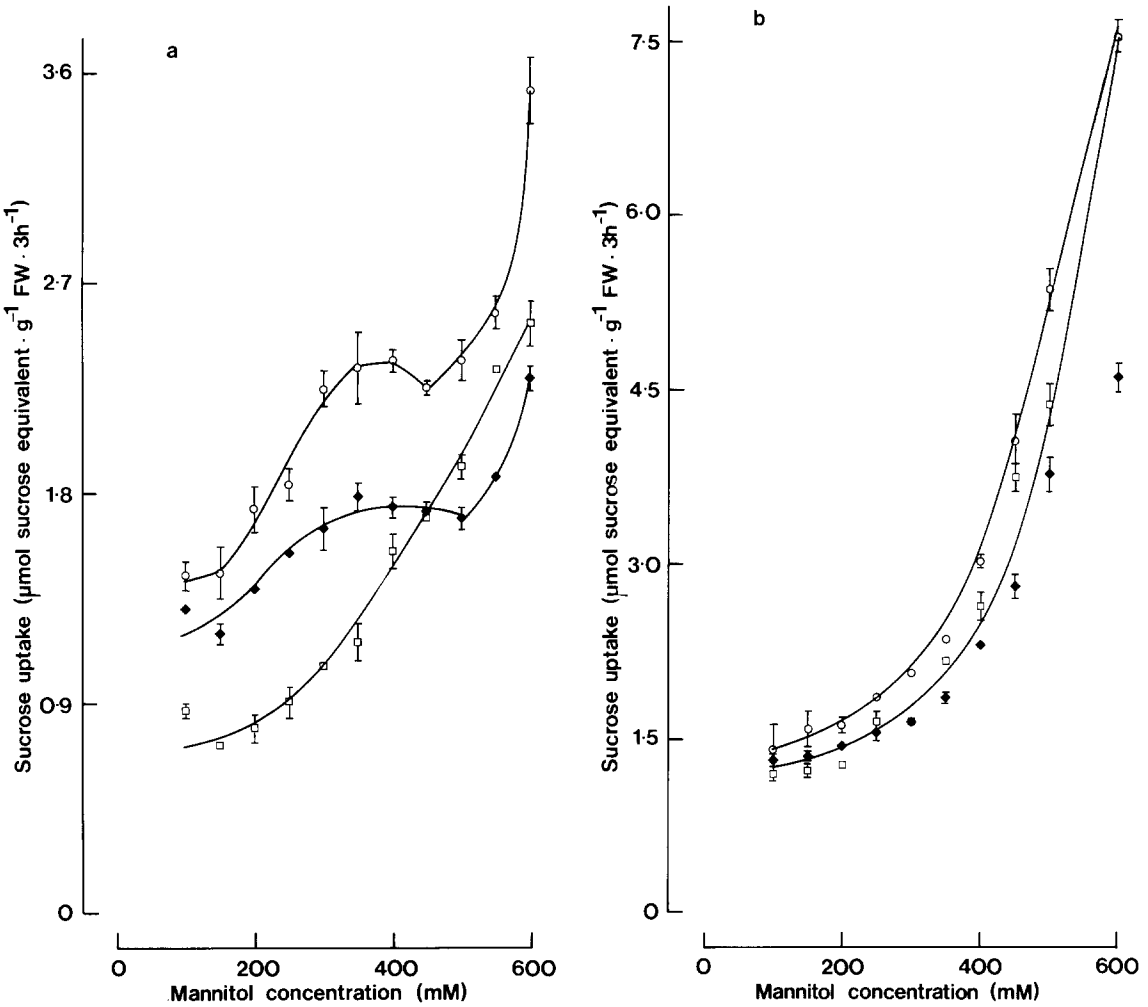

Fig. 4a, b. Effect of mannitol concentration on sucrose uptake into discs of **a** sink and **b** source potato tubers. Incubation media included 50 mM sucrose, PCMBS (◆), CCCP (□) or no inhibitors (○)

kinetics are therefore most likely to represent uptake into this single cell type, the saturable component representing carrier-mediated transport at the plasmalemma and the linear component uptake by diffusion.

In source-tuber discs, uptake of sucrose also demonstrated biphasic kinetics although the saturable component was considerably less prevalent than in sink discs. In source tissue, PCMBS and CCCP inhibited sucrose uptake by the same amount but, in contrast to the sink tissue, CCCP did not alter the slope of the linear component. The slight inhibition of uptake with these inhibitors indicates that the great majority of sucrose uptake into source discs was by passive diffusion. The small saturating component in source tissues may represent either a residual amount of active uptake at the plasmalemma of the storage cells or possibly the active loading of sucrose into the internal phloem strands.

Starch synthesis. A large proportion of the total sucrose taken up by sink-tuber discs was converted to starch. Although PCMBS decreased the amount of sucrose taken up, it did not alter the proportion of sucrose partitioned to starch (see also Oparka and Wright 1988b) supporting the hypothesis that PCMBS does not penetrate the cells (M'Batchi et al. 1986). By contrast, treatment of discs with CCCP almost completely eliminated starch synthesis, probably due to the general uncoupling of membrane-bound ATPases required for starch synthesis. Interestingly, the amount of starch synthesised in CCCP-treated sink discs was comparable to that found in untreated source discs, indicating that this represented the basal level of starch synthesis in both sink and source tubers. In source discs, sucrose uptake was maintained at a rate approximately equivalent to that seen in PCMBS-treated sink discs (85% of uptake into control sink tissue at 100 mM exogenous sucrose). However,

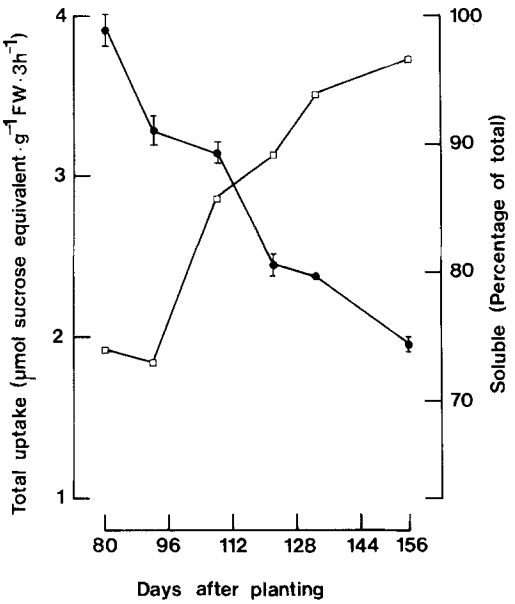

Fig. 5. Total sucrose uptake (●) and the percentage remaining as sucrose (□), in potato tuber discs incubated for 3 h in 50 mM sucrose, 9.25 kBq·ml^{-1} [^{14}C]sucrose, 250 mM mannitol and 25 mM Mes pH 6.5. Discs were cut from field-grown tubers at two-week intervals throughout the growing season

the storage cells were not able to utilise the sucrose present to synthesise starch, indicating that starch synthesis was inactivated in these tubers.

Sucrose uptake and tuber growth. The results obtained for potato tubers which had been growing in the field demonstrated that the ability to convert sucrose to starch declined as the tubers aged. This agrees with previous data on the partitioning of ^{14}C assimilates (Oparka 1985) which demonstrated that the proportion of current assimilate partitioned into starch decreases progressively during a growing season.

Turgor sensitivity. We have demonstrated previously that the uptake and partitioning of sucrose in storage tissues is turgor-sensitive, sucrose uptake and starch synthesis being optimised at low but positive cell turgors (Oparka and Wright 1988b). In that study, PCMBS reduced total sucrose uptake but the turgor response was still evident. However, turgor sensitivity was eliminated when the discs were treated with CCCP, indicating that the sensitivity of sink tissue to turgor is not mediated through the PCMBS-sensitive sucrose carrier. Instead, the data support the conclusions of Wyse et al. (1986) and Daie (1987b) that enhanced sucrose uptake at low turgor is mediated through the plasmalemma H^+-ATPase, the activity of which is inhibited at high turgor. The inhibition of turgor sensitivity by CCCP in sink potato tubers, and the lack of turgor sensitivity in source tubers, implies that it is the H^+-ATPase on the plasmalemma of the storage-parenchyma cells which mediates the response of sink tissues to turgor. Support for the location of intense ATPase at this site has been shown previously by cytochemical means (Oparka 1986). The results obtained with tubers of different ages show that, in addition to a decrease in starch-synthesising capacity, there appears also to be a loss of carrier-mediated sucrose-uptake capacity, presumably because of the gradual loss of ATPase activity (and hence turgor sensitivity) at the plasmalemma.

In-vitro versus in-vivo sucrose transport. The results show that in isolated sink-tuber tissues a large proportion of the sucrose taken up is transported across the plasmalemma by active, carrier-mediated transport into storage cells whilst, in contrast, sucrose uptake into source tissues is almost entirely diffusional. The significance of these observations in relation to the in-vivo transport of sucrose in the tuber is as yet unclear. One possibility is that sucrose, unloaded apoplastically, is taken up into individual storage cells across the plasmalemma in a manner similar to that reported for wheat grains by Ho and Gifford (1984). However, the symplastic unloading pathway demonstrated previously (Oparka 1986; Oparka and Prior 1987) appears to be contradictory to the presence of a mechanism for active, carrier-mediated uptake of exogenous sucrose from the apoplast. One possibility is that the latter represents a retrieval mechanism for sucrose lost to the apoplast (Maynard and Lucas 1982). Browning et al. (1980) have suggested that the ATPase activity in sink tissues, localised cytochemically, may function to ensure that sucrose which is moving symplastically is retained within the plasmalemma.

We suggest that in sink potato tubers, sucrose is unloaded symplastically and diffuses down a concentration gradient from the sieve element to the cytoplasm of the storage cells. The continuing conversion of sucrose to starch in the amyloplasts would ensure the maintenance of this gradient (see also Ho 1986). However, not all of the unloaded sucrose is converted to starch, a proportion entering a vacuolar storage pool (Mares et al. 1985). In this situation an active uptake mechanism would be required to retrieve sucrose lost to the apoplast by diffusion. Such a mechanism for retrieval of escaped sucrose following symplastic unloading has recently been proposed by Stanzel and coworkers (Stanzel et al. 1988).

It appears that prior to sprouting there is a marked alteration in the mechanisms associated with sucrose uptake, the ability of the storage cells to take up sucrose from the apoplast by an active mechanism being lost. The pathways and mechanisms of phloem loading in the source tuber are the subject of further investigations in our laboratory.

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Received 9 June; accepted 20 October 1988