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GABRIELA LORENC-PLUCIŃSKA AND TOMASZ BOJARCZUK

Regulation of sugar transport in poplar leaves

Abstract

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The mechanism of sucrose and hexose transport was studied in tissue discs isolated from source leaves of *Populus deltoides*, *P.* 'Marilandica', *P.* 'Virginiana de Frignicourt' and *P.* 'Forndorf'. It was found that sucrose was taken up by the tissue discs in preference to glucose and 3-O-methylglucose (3-OMG). Kinetic analysis of [^{14}C]sucrose loading revealed the presence of two transport components: a saturable and a linear component. The saturable component was greatly inhibited by carbonyl cyanide-m-chlorophenylhydrazone (CCCP), p-chloromercuribenzenesulfonic acid (PCMBS) and alkaline pH. Active transport of sucrose was temperature-dependent and substrate specific. In contrast, the kinetic profiles for D-glucose and 3-OMG uptake were linear with no saturation and without notable sensitivity to CCCP or temperature and pH requirements.

Additional key words: glucose uptake, *Populus*, sucrose uptake.

Address: G. Lorenc-Plucińska, T. Bojarczuk, Polish Academy of Sciences, Institute of Dendrology, 62-035 Kórnik, Poland.

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INTRODUCTION

Depending on the plant species, endogenous and environmental conditions, transport of photosynthates from the mesophyll cells into the sieve tubes in leaves could be apoplastic and/or symplastic (Giaquinta 1983, Van Bel 1987, 1989, Delrot 1989). Based on studies of the structure of leaf minor veins in 700 species, Gamalei (1985, 1988, 1989, 1991) suggests that symplastic loading is more ancient and more economical for plants. However phloem loading via the apoplast is more efficient under unfavorable conditions.

The loading mechanism of assimilates into the phloem in trees is poorly understood. Although there are many studies on *Populus deltoides* (Dickson and Larson 1981, Dickson and Nelson 1982, Vogelmann et al. 1982, Isebrands and Nelson 1983, and literature cited therein), these studies were conducted on the sink to source relations of *Populus* leaves, rather than on the transport mechanism of assimilates.

This paper describes mechanisms of sugar uptake in mature leaves of different cultivars of *Populus deltoides*. The poplar clones were chosen for this study considering their interesting differentiation in susceptibility to air pollution and heavy metal contamination in the soil (Rachwał and Kluczyński 1987).

MATERIALS AND METHODS

The studies were carried out on 20-year-old trees of *Populus deltoides*, *P.* 'Marilandica', *P.* 'Virginiana de Frignicourt', *P.* 'Forndorf' growing in experimental plots of the Institute of Dendrology in Kórnik (52°15′ W / 17°06′ E). *Populus deltoides* is a species with a large geographical distribution in North America while the cultivars are clones of intrasectional hybrids, the so-called Canadian poplars (Euroamerican, *Aigeiros* × *Aigeiros*). Each of the clones was represented by one tree.

Tissue preparation

For the studies only young, fully expanded leaves were used. These leaves are the major source of photosynthate for growth and development in poplars (Isebrands and Nelson 1983). The leaves were collected from exposed areas of the tree crown and transferred with their petioles in H_2O to the laboratory. Leaf discs 8 mm in diameter were cut from intercostal areas with a cork borer.

The tissue discs were neither pelled nor abraded. The stripping of larger areas of the lower epidermis of poplar leaves created problems and led to greater destruction of the leaf blade. There were attempts to use tissue discs cut from leaves abraded with carborundum. However, we observed in some experiments that the edges or sides of leaf discs cut from carborundum-treated leaves became discolored which caused great variability in sugar uptake rates. So, the presence of epidermis was in our studies a kind of diffusion barrier for transported sugar (Delrot 1989).

The discs were transferred to a vacuum flask containing a preincubation solution of 0.25 mol m^{-3} $MgCl_2$, 0.5 mol m^{-3} $CaCl_2$, 250 mol m^{-3} mannitol and 25 mol m^{-3} 2-(N-morpholino)ethanesulfonic acid (MES) buffer (pH 5.0). They were vacuum infiltrated until the discs no longer floated on the preincubation medium. The buffer medium was then exchanged for fresh buffer and the discs were aerated at 20°C for 60 min.

Sugar uptake

Studies of sugar uptake were performed using the method of Lorenc-Plucińska and Ziegler (1989) with some modification. Briefly, if not indicated otherwise, the leaf discs were incubated for 30 min in a medium containing 0.25

mol m^{-3} $MgCl_2$, 0.5 mol m^{-3} $CaCl_2$, 25 mol m^{-3} MES-NaOH (pH 5.8), 250 mol m^{-3} mannitol, [U-^{14}C]-sugars, with or without CCCP and PCMBS – details are given in the legends to figures. [^{14}C] sugars were supplied in a background of unlabelled sugars. Separate experiments were conducted for [^{14}C] sucrose, [^{14}C]glucose and [^{14}C]3-OMG. Upon completion of each incubation the discs were washed 3 times with unlabelled solution for 2 min each, decolorised and digested in 70% (v/v) perchloric acid and 30% (v/v) H_2O_2 for 90 min at 70°C. The radioactivity was determined using liquid scintillation counting. All counts were corrected for background and quenching.

To manipulate the pH of the solutions, various buffers (25 mol m^{-3}) were used in both the preincubation and incubation media (details are given in the legend to Fig. 5) All experiments were performed in the dark in a shaker bath (80 shakes min^{-1}).

The chemicals used were: [U-^{14}C]-sucrose (spec. act. 19.8 GBq/mmol), D-[U-^{14}C]-glucose (spec. act. 10.3 GBq/mmol) and [U-^{14}C]-3-O-methyl-glucose (spec. act. 10.2 GBq/mmol) from Radiochemical Center Amersham, CCCP, PCMBS, HEPES, MES, Tricine, mannitol from Sigma [St. Louis, USA]; all other chemicals were analytical grade from Merck (Darmstadt, Germany).

RESULTS

Time course of sugar uptake

Under our experimental conditions, accumulation from an external solution of 5.0 mol m^{-3} sucrose and glucose was linear from 0 to 45 min (Fig. 1).

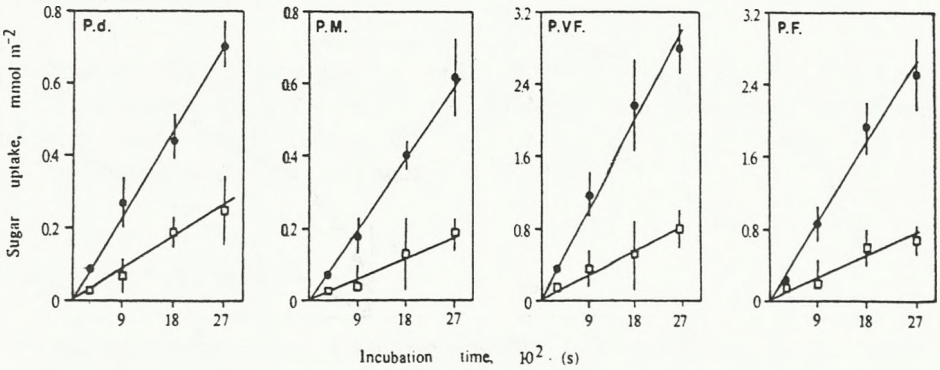

Fig. 1. Time course of sucrose (o) and glocose (□) uptake into tissue discs of poplar in a 5 mol m^{-3} external sugar solution (pH 5.8, 25°C). Each value is the average ±SD of three independent experiments. P.d.: *P. deltoides*, P.M.: *P.* 'Marilandica', P.VF.: *P.* 'Virginiana de Frignicourt', P.F.: *P.* 'Forndorf'.

Among the leaves of the poplars assayed, the uptake rate of sucrose was at least three times higher than that of glucose. It is important to note that uptake of radioactivity from sucrose and glucose by freshly excised leaves was about four times higher in *P.* 'Virginiana de Frignicourt' and *P.* 'Forndorf' than in *P. deltoides* and *P.* 'Marilandica'.

Concentration dependence of sugar uptake

Analysis of the concentration dependence of sugar uptake into leaf discs of the four poplar clones indicated the presence of two different pathways of uptake. Sucrose uptake showed a biphasic dependence: a saturable component was apparent at low external sucrose concentrations with a linear, nonsaturable component of uptake predominating at higher sucrose concentrations (Fig. 2 and 3). An analysis of sucrose uptake rate conducted in presence of

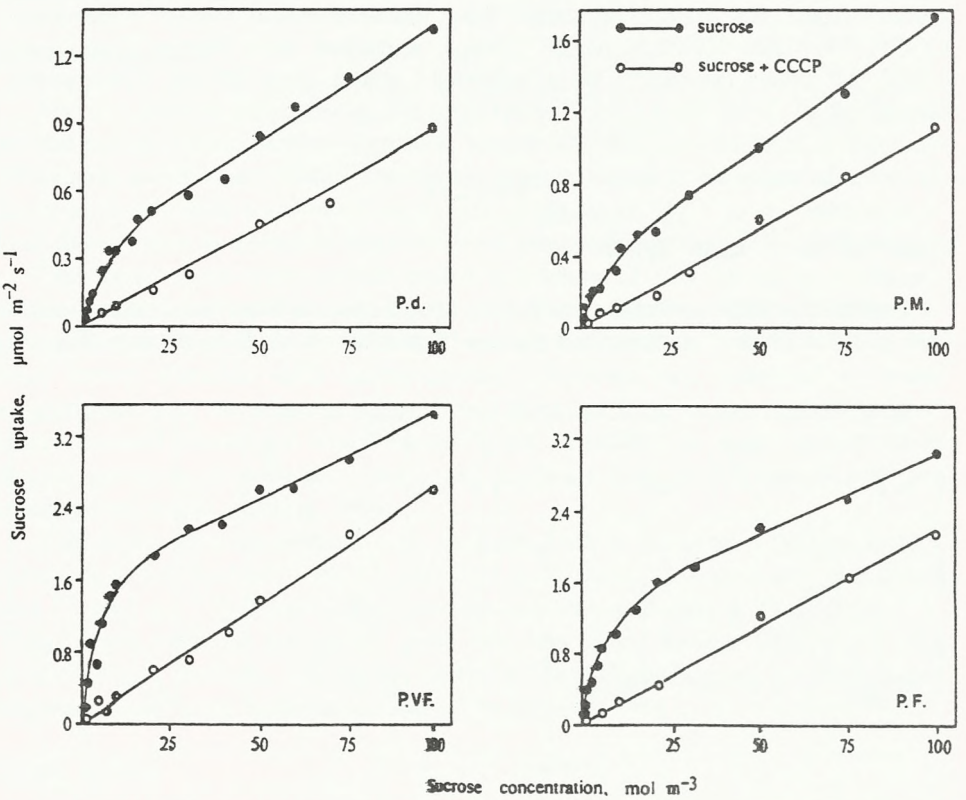

Fig. 2. Concentration dependence of sucrose uptake into poplar leaf discs at pH 5.0 (22°C) with and without 5 mmol m^{-3} CCCP. Each value is the average of three (P.d.), six (P.M.), four (P.VF.) and five (P.F.) independent experiments. Others: see Fig. 1.

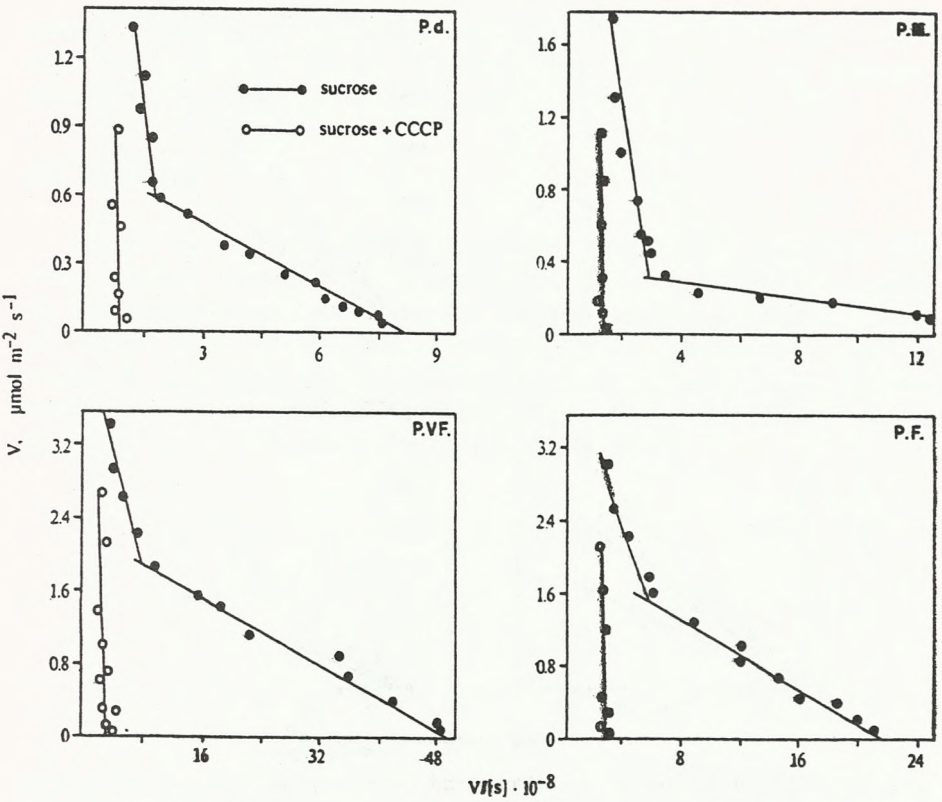

Fig. 3. Eadie-Hofstee transformation of sucrose uptake data presented in Fig. 1. At pH 5.0 K_m (mol m^{-3}) and V_{max} (μmol $m^{-2}s^{-1}$) for the saturable uptake component were: 8.65 ± 1.44 and 0.68 ± 0.08 for P.d., 2.04 ± 0.49 and 0.41 ± 0.04 for P.M., 4.54 ± 0.5 and 2.42 ± 0.39 for P.VF. and 9.7 ± 1.75 and 2.14 ± 0.28 for P.F.

5 mmol m^{-3} CCCP demonstrated only a linear first-order uptake (Fig. 2 and 3). On the other hand, D-glucose and 3-OMG enters as a linear function of external sugar concentration and the uptake of D-glucose exceeds that of 3-OMG even under the influence of CCCP (Fig. 4).

Temperature dependence

The rate of glucose and sucrose uptake into leaf discs of the four poplar cultivars from the 1.0 mol m^{-3} sugar solution is dependent on the temperature of incubation medium (Table 1). Sugar transport rates were substantially inhibited at 10°C, whereas the uptake at 20 and 30°C were not different. Between 10 and 20°C, the Q_{10} values ranged from 3.5 to 4.3 for sucrose with

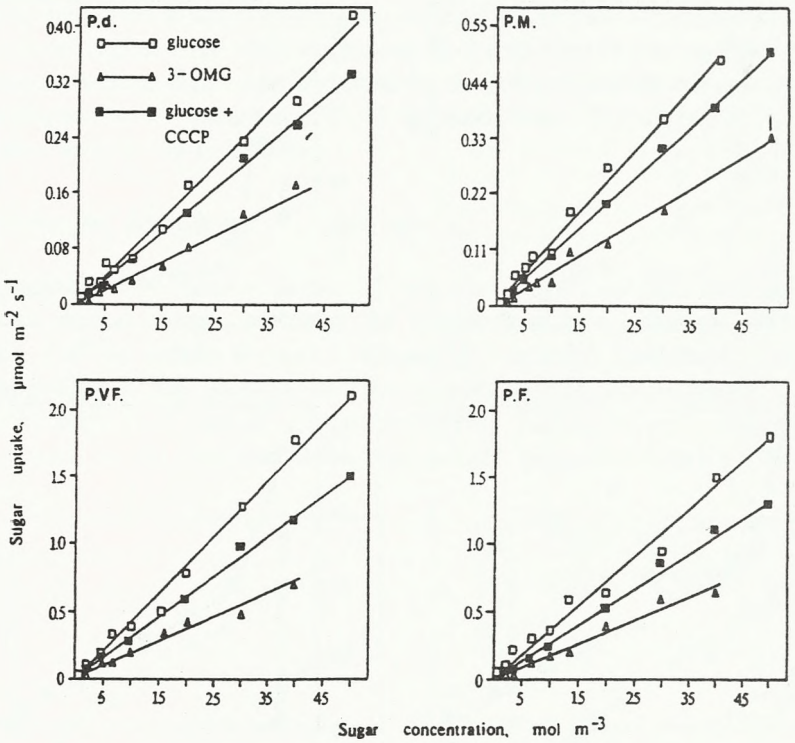

Fig. 4. Concentration dependence of D-glucose and 3-OMG uptake at pH 5.0 (22°C) in the presence or absence of 5 mmol m^{-3} CCCP. Each point is the mean (±SD) of three independent experiments. Others: see Fig. 1.

Table 1

Effect of incubation temperature on uptake of 1 mol m^{-3} sucrose and glucose. Leaf discs were incubated in MES-buffer medium pH 6. Pretreatment temperature was the same as incubation temperature. Data are means from two experiments with three replications each.

Temperature	*P. deltoides*	*P.* 'Marilandica'	*P.* 'Virginiana de Frignicourt'	*P.*'Forndorf'
°C	Sucrose, nmol m^{-2} s^{-1}			
10	24± 2	28± 2	142±17	64± 8
20	97±21	125±17	501±40	209±23
30	132±12	154±14	515±61	243±24
Q_{10}(10°–20°C)	4.12	4.34	3.61	3.45
E_{act}(kJ·mol^{-1})	92±11	99±15.6	84±10.7	79±11.7
°C	Glucose, nmol m^{-2} s^{-1}			
10	18± 4	17± 5	52±10	32± 5
20	34± 7	29± 5	79±10	57± 9
30	48± 7	36± 5	87±18	79±18
Q_{10}(10°–20°C)	1.93	1.7	1.58	1.82
E_{act}(kJ·mol^{-1})	41± 8.7	39± 7.6	32± 7.7	38± 6.1

corresponding apparent activation energies from 80 to 100 kJ·mol^{-1}. On the other hand, the Q_{10} values for glucose were less than 2, and energies of activation were from 38 to 41 KJ·mol^{-1} (Table 1).

pH dependence

The pH dependence of sucrose and glucose uptake was examined at various concentrations of sugar in the external solution (Fig. 5 and 6). In leaf discs of the four poplars, the maximal sucrose accumulation rate was observed at acidic pH values (from pH 5 to pH 6), while uptake at alkaline pH values was negligible. In contrast, glucose uptake from a 0.5 mol m^{-3} external solution exhibits no pH dependence. Similarly, the uptake of 50 mol m^{-3} sucrose remained unchanged over a wide pH range (4.0-7.0).

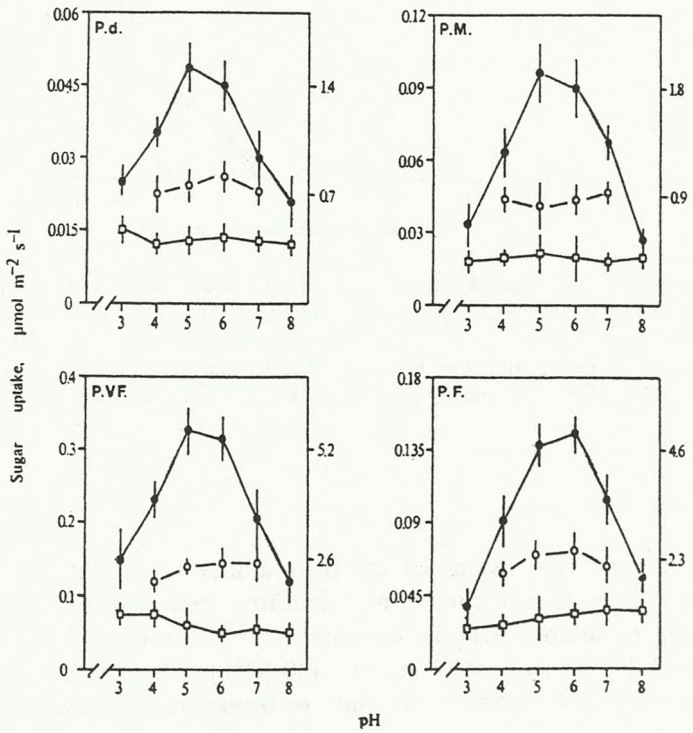

Fig. 5. Effect of external pH on the rate of sugar uptake. Left ordinate axis: (o) 0.5 mol m^{-3} sucrose and (□) 0.5 mol m^{-3} glucose; right ordinate axis: (o) 50 mol m^{-3} sucrose. Discs were preincubated for 20 min with a buffer medium at the desired pH, then they were incubated for 30 min in a solution of ^{14}C-sugars at the appropriate pH at 22°C. Citrate-phosphate buffer was used at pH 3 and 4, MES at pH 5 and 6, HEPES at pH 7 and Tricine at pH 8. Data are means ±SD from at least four experiments. Others: see Fig. 1.

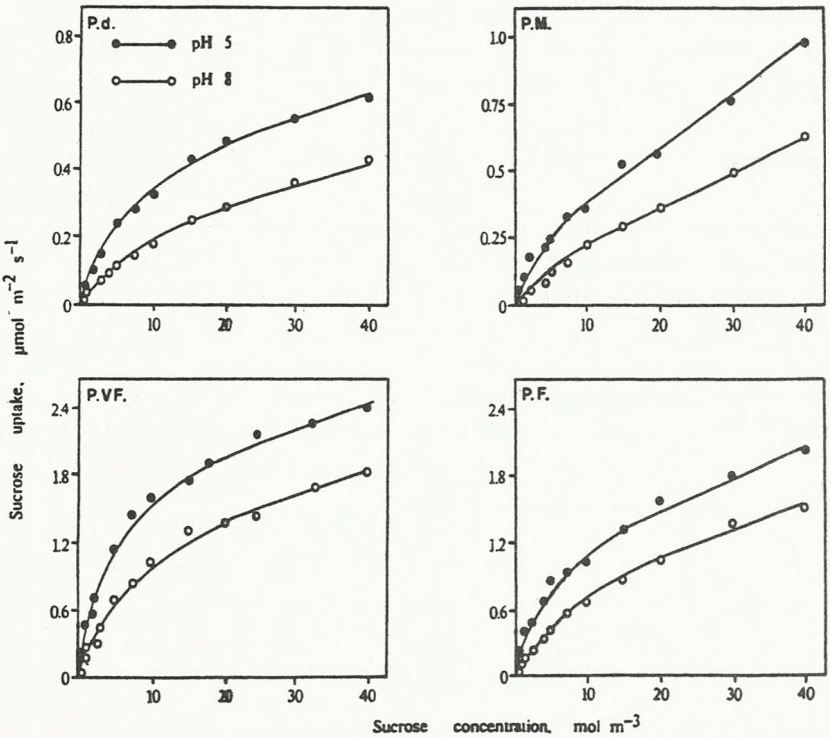

Fig. 6. Concentration dependence of sucrose uptake at pH 5 and 8. Tissue discs were preincubated and incubated in a 25 mol m^{-3} MES (pH 5.0) or Tricine (pH 8.0) buffer medium at 22°C. Data for pH 5.0 are from Fig. 1. The data for pH 8.0 are means of at least five independent experiments. At pH 8.0 K_m (mol m^{-3}) and V_{max} (μmol $m^{-2}s^{-1}$) were: 25.0±5.0 and 0.69±0.07 for P.d., 6.4±0.8 and 0.44±0.06 for P.M., 12.5±1.75 and 2.5±0.24 for P.VF. and 19.4±3.1 and 2.09±0.34 for P.F. Others: see Fig. 1.

Substrate specificity

Several sugars were examined for their ability to inhibit the uptake of ^{14}C-sucrose (Table 2). The competing substrates were present at 25 times the concentration of sucrose. Uptake of 2 mol m^{-3} ^{14}C-sucrose into tissue discs was inhibited by 50 mol m^{-3} sucrose (40-50%), whereas the influence of glucose, fructose and galactose on sucrose transport was negligible.

PCMBS sensitivity

The nonpenetrating, protein-modifying reagent PCMBS inhibited sucrose uptake into tissue discs of *Populus* (Fig. 7). The extent of this inhibition was dependent on the sucrose concentration in the external solution and the

Table 2

Competition of several sugars with ^{14}C-sucrose uptake into leaf discs of *Populus* sp. The labelled sucrose (2.0 mol m^{-3}) was added in MES-buffer medium (pH 5.7, 25°C) just before the competitors (50 mol m^{-3}) and the uptake lasted 30 min. The results are means (±SD) of four different experiments.

Unlabelled compounds	*P. deltoides*	*P.* 'Marilandica'	*P.* 'Virginiana de Frignicourt	*P.* 'Forndorf'
	Sucrose uptake, nmol m^{-2} s^{-1}			
None (control)	119±14	183±31	694± 97	333±60
Sucrose	61± 5	82±11	278± 47	160±24
Glucose	95±13	174±32	625±128	260±29
Fructose	125±25	142±34	603± 54	361±52
Galactose	103±12	187±29	582± 82	296±42

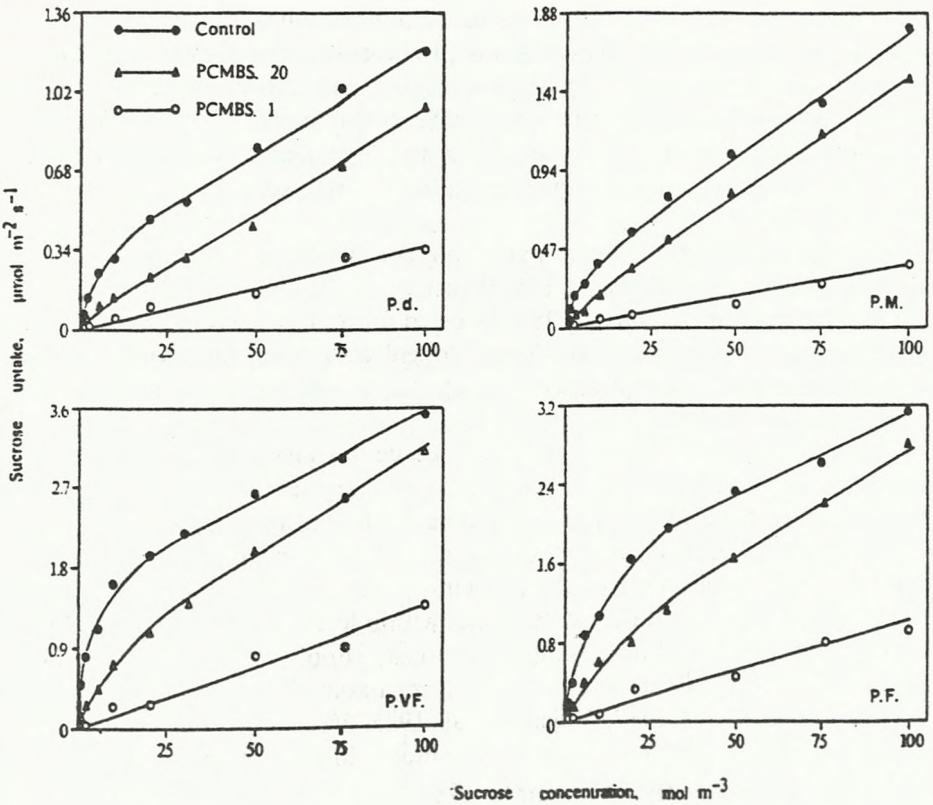

Fig. 7. Effect of PCMBS on the concentration-dependent kinetics of sucrose uptake into tissue discs. The inhibitor was present in the incubation solution (MES-buffer medium, pH 5.7, 22°C) in concentrations of 20 mmol m^{-3} and 1 mol m^{-3}. Control – without PCMBS. The data are means from four different experiments. Others: Fig. 1.

concentration of sulfhydryl reagent used. The low concentration of PCMBS (20 mmol m^{-3}) inhibited the saturable component of sucrose uptake while the linear component of uptake was only slightly affected (Fig. 7). The high concentration of PCMBS (1 mol m^{-3}) in the incubation medium significantly reduced the linear and completely eliminated the saturable component of sucrose uptake into tissue discs (Fig. 7).

DISCUSSION

Despite the numerous papers on assimilate transport in poplars, the pathway of phloem loading in leaves in this species is unknown. From structural and plasmolytic studies, one could postulate that there is a functional symplastic route for photoassimilates from the mesophyll cells to the sieve-element companion cell complex of minor veins, because: 1) leaves of *Populus deltoides* have large numbers of plasmodesmata and they are present in all the walls between the palisade parenchyma cells and the sieve tubes of the minor veins (Russin and Evert 1984, 1985); 2) Gamalei (1988, 1989) found the presence of an open type of minor vein and high plasmodesmatal frequency between mesophyll and companion (intermediate) cells for *Salicaceae* (including *Populus*).

On the other hand, in a paper on the structure of companion cells associated with sieve elements, the frequency of plasmodesmata and pathway for phloem loading, Gamalei (1985) reported for *Salicaceae* (including *Populus*) mixed types of companion cells (type I 'open' with many plasmodesmata and type II 'closed' with few plasmodesmata), with mixed types of phloem loading (symplastic/apoplastic).

Results of our studies suggest that in tissue discs isolated from leaves of *P. deltoides*, *P.* 'Marilandica', *P.* 'Virginiana de Frignicourt' and *P.* 'Forndorf' loading of sucrose in the phloem occurs from the apoplast.

The use of leaf discs for studying the mechanism of sugar uptake, interpreted as a reflection of the phloem loading process, has been criticised due to the presence of different cell types within leaf discs (Delort 1989, Orlich and Komor 1992). In this system, exogenously supplied sucrose can be taken up by mesophyll cells as well as by phloem tissue (Fondy and Geiger 1977, Maynard and Lucas 1982, Wilson et al. 1985, Van Bel 1989). Nevertheless, unlike mesophyll uptake of sugar, only phloem loading is specific for sucrose and is PCMBS-sensitive (Giaquinta 1983, Delrot 1989).

In agreement with Delrot (1989) we assumed that the fundamental characteristics for the apoplastic phloem loading pathway are: active and carrier-mediated loading, saturation kinetics, selectivity and sensitivity to PCMBS.

In four different poplar cultivars a sucrose-uptake versus sucrose concentration analysis indicated biphasic kinetics consisting of a carrier-mediated saturable (active) component conforming to Michaelis-Menten kinetics at low sugar concentrations plus a linear component operating at high sugar concentrations [Fig. 2 and 3]. Active sucrose uptake was temperature-dependent and the carrier-mediated component was inhibited to a significant extent at low temperature [Table 1]. The Q_{10} values ranged from 3 to 4, suggesting a carrier-mediated process.

Sucrose transport in poplar tissue discs was energy and proton dependent. This was indicated by sucrose uptake inhibition under the influence of the metabolic uncoupler CCCP [Fig. 2] and by pH sensitivity [Fig. 5 and 6]. The uncoupler CCCP reduces active sugar uptake by inhibiting ATP supply, dissipating the proton gradient across the membrane, depolarising the membrane potential and inhibiting the sugar H^+-cotransport system in plants [Giaquinta 1983, Delrot 1989]. Adding CCCP to the incubation medium caused inhibition of sucrose uptake, resulting in 82-90% reductions of the saturable component and only slight changes (20-28%) in the rate of the non-saturable component [Fig. 2 and 3].

Over the pH range (from 3.0 to 8.0) the uptake of sucrose by poplar discs was strictly dependent on pH of the incubation medium (Fig. 5 and 6). Sucrose uptake from a 0.5 mol m^{-3} external solution (in contrast to a 50 mol m^{-3}) was markedly inhibited by acid (4 and in particular 3) and by alkaline (7 and 8) pH. This may indicate that the effect of proton availability on sucrose uptake is connected with changes in the activity of the saturable component without essential modification of the diffusion-like component. The insensitivity of sucrose uptake at high sugar concentration to external pH was found in some other plants also [Giaquinta 1977, Delrot and Bonnemain 1981, Thorne 1982).

The proton-concentration dependence of 0.5 mol m^{-3} sucrose uptake in our material was not dependent on the buffer used, because there was no difference between the inhibition of sucrose uptake caused by the ionic phosphate buffer and by the nonpermeant zwitterionic buffers (MES, HEPES) nor between HEPES and Tricine buffer (data not shown). It is not possible to rule out the influence of different proton concentrations on the metabolic activity of tissue discs, invertase activity or membrane integrity/permeability, because no studies have been performed to assess it.

It should be emphasised that at low proton concentrations (by increasing pH), the inhibition of sucrose uptake was dependent on sucrose concentration [Fig. 6]. The kinetic constants indicated that the K_m of the carrier for sucrose uptake increased at alkaline pH from 1.5 to 3.2 times whereas V_{max} was essentially unaffected [Fig. 3 and 6]. These results may be interpreted as indicating that the inhibition of sucrose uptake in alkaline pH results from

a lack of available protons as a driving force for a proton-sucrose-symport (Giaquinta 1983).

Substrate recognition by sucrose carriers in plant systems were recently documented in detail (Delrot 1989). In our plant material, the specificity of the sucrose uptake system can be derived from the competition studies [Table 2]. Uptake of ^{14}C-sucrose into the tissue discs of poplars was not inhibited by different hexoses. The alternate-substrate inhibitors of ^{14}C-sucrose uptake were added into the incubation medium with tissue discs a few seconds before the addition of ^{14}C-sucrose, therefore they could not be accumulated in the cell and induce a feedback effect on rates of sucrose uptake. For that reason our results seem to indicate that the carrier of sucrose does not interact with hexoses and that sucrose uptake into poplar leaf discs is specific.

PCMBS, an impermeable sulfhydryl reagent inhibits phloem loading of exogenously supplied and endogenous sugar, with or without changes in the proton pump activity and membrane potential (Delrot 1989, Bourquin et al. 1990). On the other hand PCMBS does not affect the symplastic pathway of sugar transport (Madore et al. 1986, Madore and Lucas 1987, Van Bel et al. 1992). In our work, the inhibition of sucrose uptake by PCMBS was dependent on sucrose as well as on PCMBS concentration (Fig. 7). A low concentration of PCMBS reduced essentially only the saturable component of sucrose uptake, but a high concentration inhibited both components of the uptake system. The nature of this inhibition requires further investigation. However a similar mechanism of sucrose uptake inhibition by different PCMBS concentrations (and by a metabolic uncoupler, Fig. 2) was described earlier by Schmitt et al. (1984). According to these authors, this type of result indicates that the uptake of sucrose consists of a saturable and a linear component, and this latter is considered to be the sum of a non-saturable, carrier-mediated system and a diffusion process.

The mechanism of glucose uptake into leaf discs of poplars differed significantly in terms of kinetics and energetics from the system involved in sucrose uptake. Glucose and 3-OMG were accumulated as a linear function of external sugar concentration (Fig. 4). Glucose transport remained independent of pH changes (Fig. 5), temperature (Table 1) and the presence of CCCP (Fig. 4). These results lead to the postulation that glucose uptake is passive.

In many species, the driving force for phloem loading is a sucrose-proton-symport (Giaquinta 1983, Delort 1989). A similar mechanism of sucrose transport is described in this report. The conclusion about the presence of a proton-sucrose-cotransport system in poplar is based on the observation of biphasic kinetics of sucrose uptake, temperature, proton and energy dependence, specificity for sucrose and PCMBS-sensitivity.

Our results are partly different compared to those of Gamalei (1988, 1989); this could be the result of differences in experimental methods and plant

material, i.e. different poplar species or leaves in different physiological status. It is known for example that the transition from the importing to the exporting stages could be accompanied by the reduction of symplastic connections between mesophyll and companion cells (Bourquin et al. 1990) and thereby the possibility of symplastic routes for sucrose transport could be reduced. Furthermore, in our studies, the buffered pre- and incubation solutions contained Ca^{++}, and this may reduce the permeability of plasmodesmata. Likewise, it is not to exclude the possibility of the coexistent of symplastic and apoplastic phloem loading (Van Bel 1989, Gamalei 1985, 1991).

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Regulacja transportu cukru w liściach topoli

Streszczenie

Badano mechanizm transportu sacharozy, D-glukozy i 3-O-metyloglukozy (3-OMG) w krążkach liściowych izolowanych z liści *Populus deltoides* i jej mieszańców euroamerykańskich *P.* 'Marilandica', *P.* 'Virginiane de Frignicourt' i *P.* 'Forndorf'.

U wszystkich wyżej wymienionych topól, mechanizm pobierania egzogennie podanego cukru przez krążki liściowe był jednakowy.

Pobieranie sacharozy przez krążki liściowe zachodziło we współtransporcie z protonem. W procesie tym stwierdzono obecność dwóch komponentów transportu: w małych stężeniach egzogennie podawanej sacharozy, odpowiedzialny za transport był komponent wysycony; w stężeniach wyższych niż 10 mM pobieranie sacharozy było zdominowane przez niewysycony, liniowy, dyfuzyjnopodobny komponent. Komponent wysycony był hamowany przez karbonylocyjanek m-chlorofenylohydrazonu, kwas p-chlororтęciobenzenosulfonowy i alkaliczne pH. Aktywny transport sacharozy zależał od temperatury środowiska inkubacyjnego i był specyficzny względem substratu.

W przeciwieństwie do powyższego, kinetyczne profile pobierania D-glukozy i 3-OMG wskazywały na pasywny transport heksoz: nie stwierdzono obecności komponentu wysyconego, uzależnienia energetycznego, wrażliwości na temperaturę i pH środowiska inkubacyjnego.

Choć mechanizm transportu cukrów u *P. deltoides* i jej odmian był jednakowy, to aktywność pobierania zarówno sacharozy jak i D-glukozy czy 3-OMG była kilkakrotnie niższa u *P. deltoides* i *P.* 'Marilandica' w porównaniu do *P.* 'Virginiana de Frignicourt' i *P.* 'Forndorf'.