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Sucrose distribution in *Populus deltoides* leaves exposed to sulfite

Abstract

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Under investigation was influence of various concentrations of sodium sulfite (0.05–7.5 mole m^{-3}) on the rates of $^{14}CO_2$ and ^{14}C-sucrose uptake, the intracellular and apoplastic sucrose content and sucrose efflux from leaf discs of *Populus deltoides*. The greatest inhibition of the rate of $^{14}CO_2$ assimilation and sucrose uptake by sulfite occurred immediately (i.e. 5 min) after the beginning of sulfite treatment and this inhibition decreased during the course of experiments. The apoplastic and intracellular content of sucrose was not changed in the first 30 min of sulfite action, but longer time of treatment causes an increase in the accumulation of sucrose in the apoplast and a decrease of the sucrose content in the intracellular compartment. On the other hand, sulfite strongly enhances the rate of release of sucrose from leaf discs during 120 min of the experiment.

Additional key words: photosynthesis, sucrose pathway.

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INTRODUCTION

One of the most sensitive effects of sulfur dioxide on higher plants is the alteration of biomass distribution over different plant organs (Lechowicz 1987). Changes in biomass partitioning due to SO_2 can be linked to the retention of photoassimilate in leaves and the inhibition of translocation of photosynthate from source-leaves to particular sinks (Taylor et al. 1986, Mooney and Winner 1988). The inhibition of sucrose export from source-leaves may result from

Abbreviations: CCCP – carbonyl cyanide-m-chlorophenyl hydrazone, HEPES – N-(2-hydroxyethyl)piperazine-N'-2-ethanesulfonic acid, K_i – inhibitor constant, MES – morpholinoethanesulfonate, PCMBS – p-chloromercuribenzenesulfonic acid, TRIS – tris(hydroxymethyl)aminomethane, Van – sodium orthovanadate.

direct damage to the apoplastic phloem loading mechanism caused by SO_2 (Gould et al. 1988, Lorenc-Plucińska 1988, Maurousset et al. 1992a).

If sucrose is even partially loaded into phloem via an apoplastic route, then sucrose synthesized in the mesophyll cells must be transferred to the cell-wall space and then actively loaded into the sieve element-companion cell complex of the phloem. Sucrose concentration in the apoplast is an important factor in the regulation of the symplast unloading and phloem loading processes. In unaffected leaves, the rate of sucrose release into the apoplast should equal the rate of sucrose taken up by the sieve tubes of the minor veins. Sucrose efflux into the apoplast may occur from the mesophyll cells, bundle sheath and vascular parenchyma (Humphreys 1988). Release of sucrose occurs by passive permeation, carrier mediated (facilitated) diffusion, or proton-sucrose cotransport driven by the proton gradient (Anderson 1983, 1986, Van Bel and Ammerlaan 1981, Van Bel et al. 1986, Secor 1987).

Although some studies have dealt with measurements of sucrose efflux from the mesophyll cells and sucrose concentration in the apoplast (Delrot et al. 1983, Ntsika and Delrot 1986, Van Bel et al. 1986) nothing is known about the influence of SO_2 and aqueous derivates (sulfite and bisulfite) on the release mechanism and sucrose content in the apoplastic compartment. On the other hand, if the retention of sugars in the leaves under the influence of SO_2 is primarily due to an inhibition of phloem loading then reduction in the activity of sucrose uptake into the minor veins should be reflected in the apoplastic and/or symplastic content of sucrose.

We have previously determined some of the characteristics of the effect of sulfite on sucrose uptake in *Populus deltoides* leaves (Lorenc-Plucińska and Figaj 1993) and therefore were interested in characterizing the influence of sulfite on sucrose release from the symplast and sucrose content in the apoplast.

MATERIALS AND METHODS

Plant material. *Populus deltoides,* Marsh. plants were grown from open-pollinated seeds for 9 weeks in a greenhouse under natural light and a day/night temperature of 22/16°C and 60-80% relative humidity. All the seeds were sown simultaneously at the end of May. As a medium, use was made of a forest soil mixed 2:1 with peat. Fully expanded leaves were harvested 3.5 h after the beginning of the light period. They were pooled to give one sample.

Labelling with $^{14}CO_2$ and ^{14}C-sucrose. Leaf discs (6 mm diameter) were excised from intercostal areas of non-abraded leaves. To allow recovery from wounding, discs were floated for 40 min on a reaction mixture containing 1.0

mole m^{-3} $CaCl_2$, 0.25 mole m^{-3} $MgCl_2$ 300 mole m^{-3} mannitol, 20 mole m^{-3} MES-buffer (pH 6.5) at 20°C. Studies of $^{14}CO_2$ fixation and ^{14}C-sucrose uptake kinetics were performed as described previously (Lorenc-Plucińska and Ziegler 1989). Briefly, the discs were incubated in a solution consisting of 20 mole m^{-3} MES or 25 mole m^{-3} HEPES, adjusted with 25 mole m^{-3} MES or TRIS to different pH-values, 0.5 mole m^{-3} $CaCl_2$, 0.5 mole m^{-3} Mg Cl_2, 300 mole m^{-3}mannitol, with or without sulfite and $NAH^{14}CO_3$ (spec. act. 2.14 GBq/mmole) in light (400 μmole $m^{-2}s^{-1}$) or [U-^{14}C]sucrose (spec. act 2 GBq/mmole) in darkness (details are given in the legends to tables and figures). The incorporation of $^{14}CO_2$ or ^{14}C-sucrose were determined by liquid scintillation counting.

Apoplastic content of sucrose. Apoplastic sucrose of *Populus deltoides* leaves was collected as described by Delrot et al. (1983). After CO_2 fixation, leaf discs were transferred to a fresh reaction mixture containing 0.5 mole m^{-3} $CaCl_2$, 0.5 mole m^{-3} $MgCl_2$, 250 mole m^{-3} mannitol (pH 6.0) and incubated for 10 min at 4°C in the dark. After that, the incubating medium was boiled for 10 min and the leaf discs were extracted three times with boiling water for 10 min. The final volume of the extract was brought to 10 ml. After cooling the incubating solution and leaf extract, each was analyzed for sucrose content by enzymatic methods adapted from Jones et al. (1977). According to Delrot et al. (1983), sucrose content of the washing medium and tissue discs corresponds with apoplastic and symplastic (intracellular) sucrose, respectively.

Efflux experiments. Immediately after 40 min preincubation to allow recovery from wounding (see above), 10 discs were incubated in 2.5 ml of medium containing 25 mole m^{-3} HEPES adjusted with 25 mole m^{-3} MES or TRIS to different pH-values, 0.5 mol m^{-3} $CaCl_2$, 0.5 mole m^{-3} $MgCl_2$ with or without sulfite. The leaf discs were incubated in light (400 μmole $m^{-2}s^{-1}$). Samples of 0.15 ml were taken from the efflux medium at specific time intervals and sucrose content was analyzed by enzymatic methods adapted from Jones et al. (1977).

RESULTS AND DISCUSSION

It has been established that the sugar transported from the mesophyll to phloem elements in poplar (*Populus* sp.) is sucrose, that phloem loading occurs from the apoplast and that sucrose enters the conducting complex via a carrier-mediated sucrose-proton cotransport mechanism (Zimmermann and Ziegler 1975, Russin and Evert 1985, Gamalei 1991, Lorenc-Plucińska and Figaj 1993). As in many other plants (Lorenc-Plucińska 1988, Maurousset and

Bonnemain 1990), the inhibition of the active loading of sucrose in *Populus* sp. by sulfite was of the non-competitive type and the calculated K_i for *Populus deltoides* was 6.41 mole m^{-3} of sulfite (Lorenc-Plucińska and Figaj 1993).

Table 1

Time-course relationship of $^{14}CO_2$ fixation leaf by discs in the presence of various concentrations of sulfite. Sulfite was added to the incubation medium (20 mole m^{-3} MES, 0.5 mole m^{-3} $CaCl_2$, 0.5 mole m^{-3} $MgCl_2$, 300 mole m^{-3} mannitol, pH 6.0) simultaneously with 5 mole m^{-3} $NaH^{14}CO_3$. Each value is the average ±SD of four independent experiments. *, **-values were significantly different from the control (without sulfite) at a 0.05 and 0.01 confidence level, respectively.

Sulfite	$^{14}CO_2$ fixation (mg C m^{-2})					
mole m^{-3}	Time of incubation (min)					
	5	15	30	60	90	120
0.0	7.1±1.2	17.8±2.8	42.7±5.5	77.9±8	124.5±10	149.4±16
0.05	6.3±1.3	16±2.0	39.3±5.9	74±9	123±16	149.4±13
0.5	4.5±0.8*	13.3±2.7	35.9±4.3	72.4±10	118.3±13	144.9±19
1.0	4.3±0.7*	12.4±1.9*	29.9±3.3*	68.6±9	105.8±16	141.9±14
2.5	3.5±0.6**	10.7±1.9*	25.6±3.6*	66.2±8	105.8±12	135.9±20
5.0	2.2±0.5**	8±1.4**	20.1±3.0**	62.3±7*	87.1±11*	121±12*
7.5	0.9±0.2**	4.4±0.6**	10.2±1.8**	50.6±6**	66.5±9**	103.1±11*

The direction of disturbances in CO_2 assimilation (Table 1) and the accumulation of sucrose in tissue discs (Table 2) under the influence of sulfite were similar. The greatest inhibition of photosynthesis and sucrose uptake by sulfite at the concentration used (0.05-7.5 mole m^{-3}) occurred immediately (i.e. 5 min) after the beginning of sulfite treatment and this inhibition decreased

Table 2

Time-course of surcose uptake into leaf discs in the presence of various concentrations of sulfite. Sulfite was added to the incubation medium (see Table 1) simultaneously with 5 mole m^{-3} ^{14}C-sucrose. Each value is the average ± SD of five independent experiments. *, **-values were significantly different from the control (without sulfite) at a 0.05 and 0.01 confidence level, respectively.

Sulfite	Sucrose uptake (mg C m^{-2})					
mole m^{-3}	Time of incubation (min)					
	5	15	30	60	90	120
0.0	11±1.3	24.3±3.3	35±5.2	122.4±12	131.3±22	155.2±19
0.05	8.3±1.2*	18.5±2.5*	31.5±3.5	110.2±14	124.7±13	152.1±26
0.5	7.7±1.3*	18.4±2.6*	26.4±3*	100.4±9*	112.9±16	136.6±14
1.0	5.5±1**	13.7±2.2**	21.0±2.7*	90.6±8*	102.4±18	127.3±18
2.5	4.2±0.9**	10.3±2**	16.1±2.6**	74.4±9**	86.7±16*	111.7±11*
5.0	2.8±0.4**	7.1±1.3**	12.2±1.7**	63.6±10**	72.2±7.2**	94.7±12**
7.5	0.6±0.1**	3.7±0.4**	7±1.3**	50.2±8**	64.3±7.7**	82.3±13**

during the course of experiments (Tables 1 and 2). The decrease of inhibition of the investigated processes with increasing time exposure to sulfite could result from the highest sulfite uptake by plant samples occurring during a very short time (i.e. from 30 s to 50 min) followed by a rapid oxidation of sulfite to sulfate (Spedding et al. 1980, Pfanz et al. 1987, Dittrich et al. 1992).

A significant inhibition of $^{14}CO_2$-fixation in light and ^{14}C-sucrose uptake in darkness was observed at concentrations of sulfite $\geqslant 0.5$ mole m^{-3} and $\geqslant 0.05$ mole m^{-3}, respectively (Tables 1 and 2). Light induces photoreductive and photooxidative detoxification mechanisms for sulfite inside the cells (Ghisi et al. 1990, Dittrich et al. 1992) and therefore the inhibiting effect of sulfite on sucrose uptake in darkness could be much more marked.

The effect of sulfite with or without various metabolic modifiers of active phloem loading, PCMBS (an impermeable sulfhydryl reagent), CCCP (a penetrating metabolic uncoupler), Van (a specific inhibitor of H^+-ATPase of plasmalemma) and of different pH on sucrose uptake (Table 3) was the same as in many other species of plants (Lorenc-Plucińska 1988, Maurousset et al. 1992a and b). For that reason it could be postulated that the inhibition of sucrose loading into leaf discs of *Populus deltoides* by sulfite is a consequence of injury of the sucrose carrier of the plasma membrane.

In contrast to CO_2-fixation and sucrose uptake, the apoplastic and symplastic sucrose content was not changed immediately (i.e. 5-30 min) after the beginning of sulfite treatment at concentrations from 0.05 to 7.5 mole m^{-3}

Table 3

Effect of pH and various chemicals on sucrose uptake into leaf discs. Chemicals were added to the medium (0.5 mole m^{-3} $CaCl_2$, 0.25 mole m^{-3} $MgCl_2$, 300 mole m^{-3} mannitol, 25 mole m^{-3} HEPES adjusted with 25 mole m^{-3} MES or TRIS to different pH-values) 25 min before sucrose (1 mole m^{-3}) and sulfite were supplied. Time of incubation with sucrose was 15 min. Data are means from 3-5 independent experiments ±SD.

pH value	Sucrose uptake (ng C $m^{-2}s^{-1}$)			
	Sulfite concentration (mole m^{-3})			
	0.0	0.05	0.5	1.0
pH 5.0	6.8±0.68	4.23±0.76	3.80±0.42	2.16±0.28
pH 6.0	8.01±1.08	6.05±0.85	5.20±0.83	4.00±0.8
pH 7.0	4.64±0.4	4.27±0.68	4.04±0.90	3.91±0.74
pH 6.0+ PCMBS, 0.5 mole m^{-3}	3.28±0.56	2.9±0.35	3.17±0.28	2.9±0.5
pH 6.0+CCCP, 0.04 mole m^{-3}	2.0±0.40	2.05±0.45	1.46±0.20	1.20±0.2
pH 6.0+Van, 0.05 mole m^{-3}	5.77±0.69	5.32±0.8	4.42±0.75	3.17±0.44

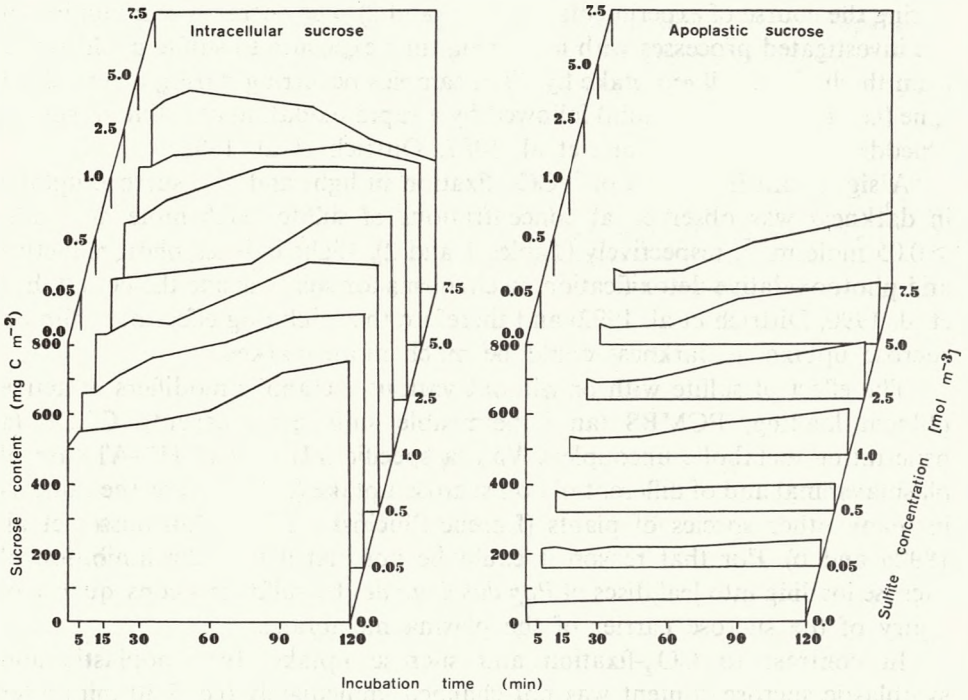

Fig. 1. Time-course of intracellular and apoplastic sucrose content in the presence of various concentrations of sulfite. The leaf discs were incubated with sulfite as described in Table 1, but without $NaHCO_3$. After incubation, the intracellular and apoplastic sucrose contents were assayed (see M & M). The intracellular and apoplastic sucrose contents in the tissue discs immediately after isolation were: 510 mg C m^{-2} and 55 mg C m^{-2}, respectively. Data are means from 2 experiments replicated 8 times.

(Fig. 1). After longer than 30 min periods of sulfite action at concentrations of $\geqslant 1.0$ mole m^{-3}, the apoplastic sucrose increased (Fig. 1). On the other hand, a significant decrease in the intracellular sucrose content took place after 90 and 120 min treatment of leaf discs with 5 or 7.5 mole m^{-3} of sulfite (Fig. 1). The observed effect of sulfite on the accumulation of apoplastic sucrose may caused by inhibition of sucrose uptake (Tables 2 and 3). The sucrose released from the symplast cannot be loaded into the conducting complex and is accumulated in the free space (Fig. 1). As a consequence, sucrose efflux from the mesophyll cells should be inhibited. The disturbances in carbon partitioning can lead to a decrease of intracellular sucrose content (Fig. 1).

The result of the present study indicates, however, that sulfite strongy stimulated the rate of release of endogenous sucrose (Fig. 2). The site and mechanism of sucrose relase into free space on its way to the sieve element companion cell complex of the phloem to be loaded is not known exactly (see Introduction). According to Van Bel et al. (1986), release of sucrose measured

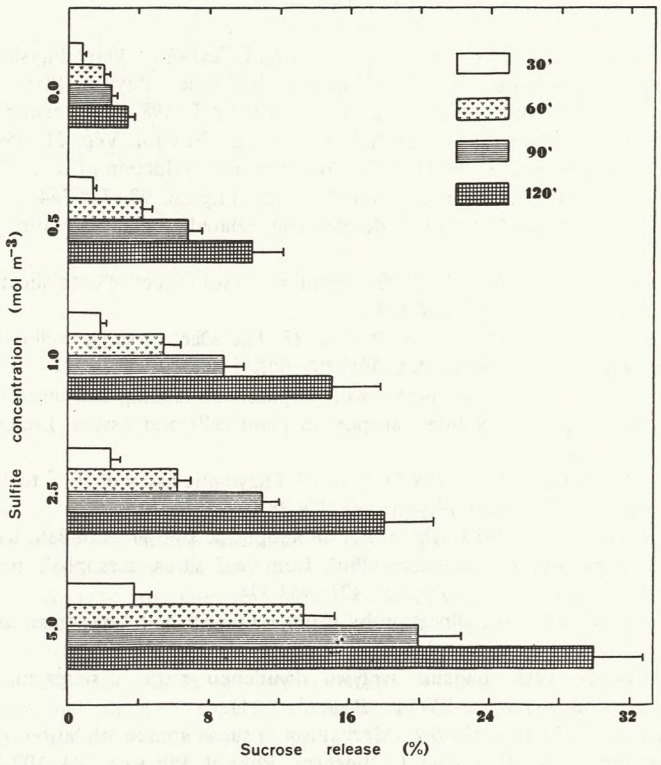

Fig. 2. Time-course study of the release of endogenous sucrose from leaf discs in the presence of sulfite. The leaf discs were incubated in 0.5 mole m^{-3} $MgCl_2$, 0.5 mole m^{-3} $CaCl_2$, 25 mole m^{-3} HEPES (pH 6.0) in the absence of sulfite (control) or with sulfite at concentrations of 0.5, 1.0, 2.5 and 5.0 mM in light. The release is expressed as the percentage of the initial intracellular concentration of sucrose. Data are means from 2-3 experiments ±SD each with 5 replication.

using the leaf-disc method is the sum of sucrose release + sucrose uptake (loading+retrieval). In this light the observed stimulation of sucrose release from tissue discs by sulfite (Fig. 2) may be due to inhibition of sucrose uptake (Tables 2 and 3). Sulfite blocks the carrier mediated sucrose loading (Maurousset et al. 1992b). Furthermore, it is not unlikely that part of sucrose release could also occur via cut veins (Turgeon 1984, Kaiser and Martinoia 1985, Van Bel et al. 1986).

On the other hand, inhibition of sucrose release as a consequence of the inhibition of phloem loading could occur in intact leaves where mesophyll-derived sucrose is effluxed into the apoplast and then entirely "withdrawn by exporting phloem" (Van Bel et al. 1986).

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Wpływ siarczynu na dystrybucję sacharozy w liściach *Populus deltoides*

Streszczenie

Badano wpływ jonów siarczynowych na natężenie asymilacji CO_2, pobieranie [U-^{14}C] sacharozy, zawartość endogennej sacharozy w symplaście i apoplaście oraz na intensywność wypływu wewnątrzkomórkowej sacharozy do apoplastu. Doświadczenia wykonano na krążkach izolowanych z całkowicie rozwiniętych i o pełnym turgorze liści 9-tygodniowych siewek topoli czarnej amerykańskiej (*Populus deltoides*, Marsh.). Krążki liściowe traktowano siarczynem sodu w stężeniach od 0.05 do 7.5 mol m^{-3} przez 5-120 min. Stwierdzono, że kierunek zaburzeń natężenia fotosyntezy i akumulacji egzogennie podawanej sacharozy w krążkach liściowych przez jony siarczynowe był podobny. Obniżenie aktywności zarówno natężenia asymilacji CO_2 na świetle, jak i pobierania sacharozy w ciemności, było największe bezpośrednio po rozpoczęciu działania jonów siarczynowych. Statystycznie istotne hamowanie włączania $^{14}CO_2$ i ^{14}C-sacharozy obserwowano w wyniku działania siarczynu w stężeniu $\geqslant$0.5 mol m^{-3} i $\geqslant$0.05 mol m^{-3}, odpowiednio. Wewnątrzkomórkowa (symplastyczna) i apoplastyczna zawartość sacharozy nie ulegała statystycznie istotnym zmianom jedynie w wyniku działania siarczynu w stężeniach od 0.05 do 7.5 mol m^{-3} przez okres 30 min. Dłuższa (60-120 min) inkubacja krążków liściowych w środowisku z siarczynem w stężeniach $\geqslant$1.0 mol m^{-3} prowadziła do wzrostu akumulacji sacharozy w apoplaście. Natomiast wewnątrzkomórkowa pula sacharozy była obniżona w przypadku traktowania krążków liściowych siarczynem w stężeniach 5.0 i 7.5 mol m^{-3} przez 90 i 120 min. Pod wpływem działania jonów siarczynowych w stężeniach od 0.5 do 5.0 mol m^{-3} przez okres od 30 do 120 min notowano również bardzo silny wzrost wypływu endogennej sacharozy z krążków liściowych do środowiska inkubacyjnego.