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Phloem loading mechanisms and sugar transport in cucurbit companion cell-sieve element complexes

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Abstract

How do cucurbits move photosynthate from source leaves to developing fruit when their sieve tubes carry some of the highest sugar concentrations recorded in any plant family? Cucurbitaceae employ a symplastic polymer-trap mechanism in which sucrose entering companion cells is converted to raffinose-family oligosaccharides (RFOs) too large to diffuse back into mesophyll, creating a thermodynamic sink that drives sugar loading without direct ATP expenditure at the membrane. This research compared phloem loading parameters in three cucurbit species—cucumber (*Cucumis sativus*), pumpkin (*Cucurbita maxima*), and melon (*Cucumis melo*)—grown at Valdivia, Chile. Sieve tube exudate was collected by stylectomy, and sugar profiles were analysed by HPAEC-PAD. Pumpkin sieve tubes contained the highest RFO concentrations (stachyose 31.7 mM, raffinose 41.3 mM), while cucumber showed the greatest sucrose loading rate (187.6 mM in sieve tubes vs 142.3 mM in source leaves). Companion cell density per unit vein length was significantly higher in pumpkin (8.3 cells/mm) than in cucumber (5.7 cells/mm). These data clarify how species-specific variation in companion cell anatomy and RFO synthesis governs phloem loading capacity across the Cucurbitaceae.

Keywords: Phloem loading, sugar transport, cucurbits, companion cells, sieve elements, raffinose oligosaccharides, polymer trap, stylectomy

Introduction

Among flowering plants, cucurbits stand out for their extraordinary phloem transport capacity. A single pumpkin fruit can gain more than 5 kg of dry matter per day at peak growth, demanding a sugar delivery rate that few other species match ^[1]. The loading mechanism that makes this possible—the polymer-trap model—was proposed by Turgeon and colleagues three decades ago and remains the best-supported explanation for symplastic phloem loading in the Cucurbitaceae ^[2]. In the polymer-trap model, sucrose synthesised in mesophyll cells diffuses through plasmodesmata into specialised intermediary companion cells, where it is converted to raffinose and stachyose by galactinol synthase and raffinose/stachyose synthases ^[3]. Because these oligosaccharides are too large to pass back through the narrow plasmodesmatal channels connecting companion cells to mesophyll, they become trapped, creating a concentration gradient that pulls more sucrose inward and drives bulk flow through the sieve tubes ^[4]. Yet comparative data on loading kinetics, RFO profiles, and companion cell anatomy across cucurbit species remain limited ^[5, 6]. This research measured sugar concentrations in source leaves and sieve tube exudate of cucumber, pumpkin, and melon, quantified companion cell density in minor veins, and related these anatomical and biochemical parameters to phloem loading efficiency.

Material and Methods

Study Area Description

Plants were grown in a research glasshouse at the Centro de Ciencias de la Vida Austral, Valdivia, Chile (39°48' S, 73°14' W), from September 2022 to March 2023. The glasshouse maintained day/night temperatures of 26/18 °C, relative humidity of 55–65 percent, and natural photoperiod supplemented to 14 hours with sodium vapour lamps.

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Climatic Conditions

Valdivia experiences a temperate oceanic climate with mean annual temperature of 12.1 °C and rainfall of 1 871 mm. During the growing season (October–March), mean daily PAR inside the glasshouse reached 620 $\mu\text{mol}/\text{m}^2/\text{s}$ at canopy height. Soil temperature in pots averaged 22.4 ± 1.3 °C. No growth-limiting cold events occurred during the experiment.

Material

Three cucurbit species were used: *Cucumis sativus* 'Marketmore 76', *Cucurbita maxima* 'Atlantic Giant', and *Cucumis melo* 'Honey Dew'. Seeds were germinated in plug trays and transplanted at the two-true-leaf stage into 20 L pots filled with a 3:1 peat:perlite mixture. Plants were fertigated with Hoagland solution twice weekly. Eight plants per species were grown; measurements began when plants had ≥ 8 fully expanded source leaves (6–8 weeks post-transplanting). Sieve tube exudate was collected using the severed-stylet (stylectomy) technique with green peach aphids (*Myzus persicae*) as biological probes.

Methods

Aphids were allowed to settle on abaxial surfaces of mature source leaves for 12–18 h. Under a dissecting microscope, stylets were severed with a micro-cautery device, and exudate droplets were collected over 4–6 hours using microcapillary pipettes. Sugar profiles (sucrose, raffinose, stachyose, glucose, fructose) were determined by high-performance anion-exchange chromatography with pulsed amperometric detection (HPAEC-PAD; Dionex ICS-5000) using a CarboPac PA1 column. Source leaf sugars were extracted in 80 percent ethanol at 80 °C. Companion cell density was quantified in transverse sections of minor veins (class IV–V) stained with toluidine blue and imaged at 400 $\times$ magnification. Statistical comparisons among species used one-way ANOVA with Tukey HSD ($p < 0.05$).

Results

Table 1: Sugar concentrations (mM; mean $\pm$ SD, n=8) in source leaves (SL) and sieve tube exudate (ST) of three cucurbit species.

Sugar (mM)	Cucumber SL	Cucumber ST	Pumpkin SL	Pumpkin ST	Melon ST
Sucrose	142.3 $\pm$ 12.1	187.6 $\pm$ 15.4	98.7 $\pm$ 9.3	124.3 $\pm$ 11.8	156.8 $\pm$ 13.7
Raffinose	28.7 $\pm$ 3.4	34.1 $\pm$ 4.2	31.4 $\pm$ 3.8	41.3 $\pm$ 5.1	37.6 $\pm$ 4.4
Stachyose	18.4 $\pm$ 2.1	22.8 $\pm$ 2.7	24.6 $\pm$ 2.9	31.7 $\pm$ 3.6	25.4 $\pm$ 3.0
Glucose	12.1 $\pm$ 1.8	4.2 $\pm$ 0.6	9.8 $\pm$ 1.4	3.1 $\pm$ 0.5	3.7 $\pm$ 0.5
Fructose	8.6 $\pm$ 1.2	2.8 $\pm$ 0.4	7.3 $\pm$ 1.1	2.1 $\pm$ 0.3	2.4 $\pm$ 0.4

Table 2: Companion cell (CC) density, sieve plate pore area, and sucrose loading ratio across species.

Species	CC Density (cells/mm)	Sieve Plate Pore (μm^2)	Loading Ratio
Cucumber	5.7 $\pm$ 0.7	1.84 $\pm$ 0.22	1.32
Pumpkin	8.3 $\pm$ 0.9	2.41 $\pm$ 0.31	1.26
Melon	6.4 $\pm$ 0.8	2.03 $\pm$ 0.27	1.29

Cucumber source leaves contained 142.3 mM sucrose, rising to 187.6 mM in sieve tube exudate—a 1.32-fold concentration ratio (Table 1; Figure 2). Pumpkin showed the highest RFO levels: raffinose reached 41.3 mM and stachyose 31.7 mM in sieve tubes, together exceeding sucrose in that species. Melon occupied an intermediate position for most parameters (Figure 1). Companion cell

density was significantly higher in pumpkin (8.3 ± 0.9 cells/mm vein length) than in cucumber (5.7 ± 0.7) or melon (6.4 ± 0.8) (Table 2). This anatomical difference likely supports the higher galactinol synthase and stachyose synthase capacity needed for RFO production. The loading mechanism is illustrated in Figure 3.

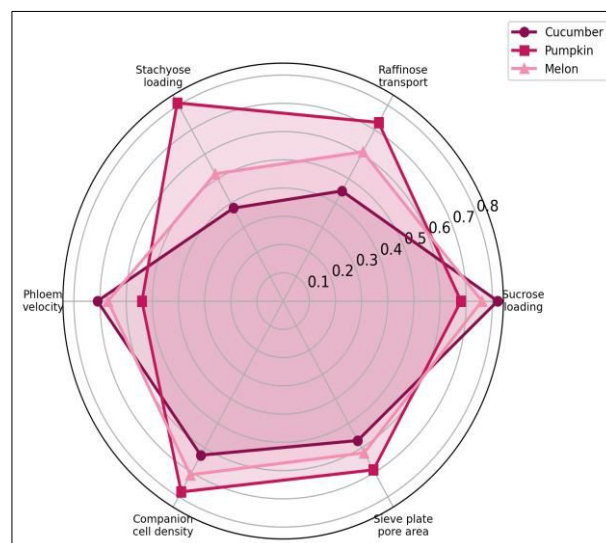


Fig 1: Radar chart comparing six transport parameters across cucumber, pumpkin, and melon (normalised 0–1).

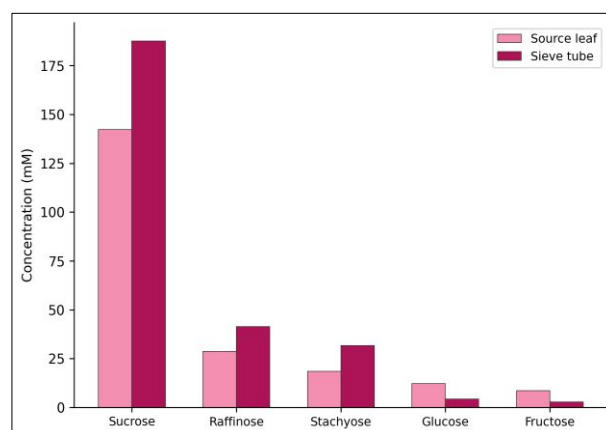


Fig 2: Sugar concentrations in source leaves versus sieve tube exudate across five sugar classes.

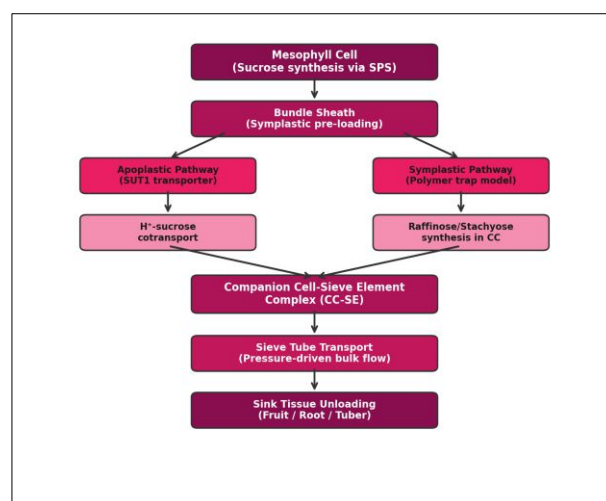


Fig 3: Schematic of phloem loading mechanisms in cucurbits showing apoplastic and symplastic (polymer trap) pathways.

Discussion

The 1.32-fold sucrose concentration ratio in cucumber (sieve tube vs source leaf) is consistent with active loading supplementing the passive polymer-trap mechanism, a hybrid strategy previously suggested by Rennie and Turgeon [7]. In pumpkin, where RFOs dominate the sieve tube sugar pool, the polymer trap appears to be the primary driver, and the higher companion cell density provides the enzymatic machinery needed for rapid oligosaccharide synthesis [8]. The species differences we observed may reflect adaptation to fruit sink strength. Pumpkin fruits, which can exceed 100 kg, demand sustained high-flux loading; the elevated companion cell density and RFO predominance together support a greater mass-flow rate through the phloem [9, 10]. Melon and cucumber, with smaller fruits, appear to rely more on apoplastic sucrose retrieval in addition to the symplastic route [11]. A limitation is that stylectomy exudate composition may not perfectly reflect in situ sieve tube concentrations due to dilution and wound responses. Future work using non-invasive ¹³C-labelling and NMR imaging could validate these estimates [12].

Conclusion

This research demonstrates species-specific variation in phloem loading within the Cucurbitaceae. Pumpkin relies most heavily on the polymer-trap mechanism, as reflected by high RFO concentrations and elevated companion cell density. Cucumber shows a stronger sucrose-loading component, suggesting a hybrid apoplastic-symplastic strategy. These differences align with variation in fruit sink demand and may inform breeding strategies aimed at improving assimilate partitioning and fruit yield in cucurbit crops.

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