

Effect of light on the regulation of carbon partitioning in mature leaves of Zea mays L.

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RECENT ADVANCES IN PHLOEM TRANSPORT AND ASSIMILATE COMPARTMENTATION

Transport libérien et compartimentation des produits de la photosynthèse Données récentes

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EFFECT OF LIGHT ON THE REGULATION OF CARBON PARTITIONING IN MATURE LEAVES OF *ZEA MAYS* L.

P. MAILLARD, J.P. ROCHER

Abstract: Biochemical analysis (carbohydrate concentration), in conjunction with compartmental analysis (size pools, transfer coefficients and fluxes), were used to evaluate the strategy of a source leaf to manage its new carbohydrate between storage and export in relation with light changes. The photoassimilate export rate tended to be buffered by an alteration of leaf carbon partitioning through changes in starch-sucrose balance in response to transfer under low or high light regimes. A priority for carbon export was observed under low light whereas the ratio of export/starch synthesis was reduced under hight light.

Résumé: Les variations d' éclairement sur la répartition et l'exportation du carbone fixé par une feuille source de maïs ont été étudiées conjointement par analyse biochimique (concentration glucidique) et analyse compartimentale (taille des pools, coefficients de transfert et flux). En réponse aux variations du niveau d'éclairement le flux d'exportation semble tamponné par ajustement de la balance saccharose-amidon. Aux faibles éclairements le flux d'exportation est prioritaire. Aux forts éclairements le flux d'exportation est relativement réduit au profit du flux d'accumulation vers l'amidon.

1. Introduction

In maize source leaves the major products of photosynthetic carbohydrate metabolism are physically compartmented. Starch synthesis and storage are performed in bundle sheath chloroplasts. Sucrose is mainly synthesized in the mesophyll cell cytoplasm and is transiently stored in vacuoles of the two leaf tissues (11). Biochemical approachs do not provide information on pool sizes and turnover rate of carbon in different cellular compartments. Compartmental analysis has been succesfully applied to quantify carbon partitioning and transfer in leaves (9, 14). Partitioning and export of assimilated carbon in leaf are regulated by environment (3, 4). Irradiance variations are know to alter photosynthesis and carbon partitioning in source leaves. The goal of the present work was to analyse the effects of transfer to low or high light regimes on CO_2 assimilation and partitioning of newly fixed carbon in maize leaf under steady state conditions.

2. Material and Methods

Maize plants (*Zea mays* L. cv F_7F_2) were grown under 300 µmol. photon m^{-2} s^{-1} (control) and transferred at the fourth mature leaf stage to low light (60 µmol. photon m^{-2} s^{-1}) or high light (700 µmol. photon m^{-2} s^{-1}) for three days. The changes of daytime carbon balance,

photoassimilate export and carbon partitioning were estimated in relation to light treatment in a source leaf. For all light treatments, pulse labelling, carbon exchange rate and estimation of assimilate export rate were performed in the mid portion of the fourth leaf. The measurements began 6 hours after the beginning of the photoperiod to ensure steady state conditions for sucrose pools. A one min $^{14}CO_2$ pulse was given, then the radioactivity in the labelled zone was continously recorded with a data acquisition system connected to a GM probe for a 10h chase. The experimental curve was fitted to a sum of three exponentials and an asymptote (13).

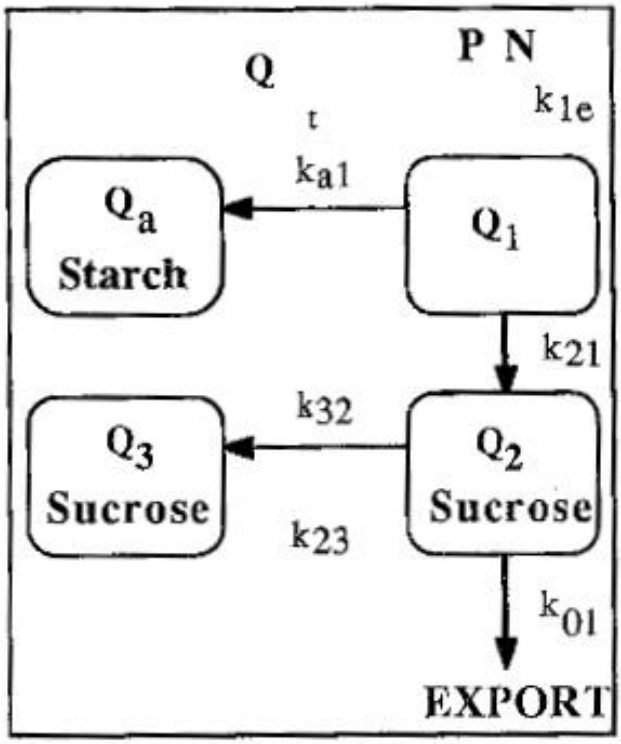


Fig. 1. Improved four compartment model for carbon distribution and export in a maize source leaf derived from the model described in Rocher and Prioul (13). PN = net photosynthesis; Q = pulse labelling; t = pulse duration; Q_1, Q_2, Q_3 = compartment sizes in mmol C $^{m-2}$.; Q_a = starch pool; k_{ij} = transfer coefficient s^{-1}.

Changes in carbon input and kinetic patterns were calculated from a four compartment model (Fig.1). The actual model was an improved version of the compartment model presented by Rocher and Prioul (13). The new model allows the calculation of transfer coefficients and compartment sizes for both sucrose and starch. Five independent fluxes were evaluated, and according to the steady state hypothesis, the algebric sum of these five fluxes was equal to the net photosynthesis, P.N. = $q_1k_{a1} + q_2k_{02}$ (JP Rocher, unpublished results). In the present paper the model was used to analyse changes on the first day of treatment.

Carbohydrates were quantified from two 0.5 cm^2 leaf discs punched from the fourth leaf at four hour intervals during the light period. Discs were quickly frozen in liquid nitrogen and carbohydrates extracted by the Dickson and Larson method (2). Biochemical carbohydrate concentrations were measured by an enzymatic method (1).

3. Results

In control light and constant irradiance, total sucrose pool (Q_2+Q_3) doubled within three hours and then stabilized to a constant value until the beginning of the dark period. Starch accumulated at a constant rate until the end of the light period (Fig. 2). Hexose content remained at a very low value throughout the light period.

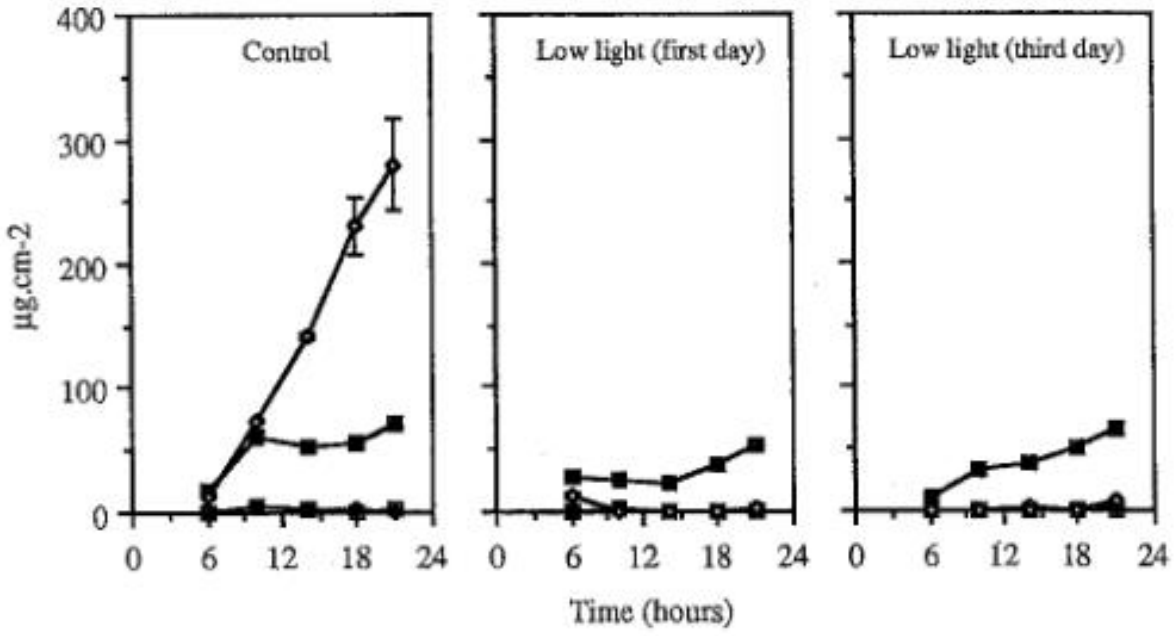


Fig. 2. Changes in the main carbohydrate pools of a fourth mature maize leaf of plants transferred from 300 µmol.photon $m^{-2}s^{-1}$ (control) to 60 µmol. photon $m^{-2}s^{-1}$ (low light) for three days. Mean ± SE from three repetitions. Error bars smaller than symbols are not shown. Fructose (◆); Glucose (□); Sucrose (■); Starch (◊).

Transfer to low light caused the starch accumulation rate to be reduced to a very low value (10% of the control from the first day after treatment), whereas the total sucrose pool remained relatively constant and equal to 30 or 57% of control (Fig. 2). This situation was not modified during the three subsequent days after the light change. Sucrose export diminished due to a decrease of carbon input but sucrose export was 92% of the photosynthetic rate as compared to 84% in control light (Table 1). This higher relative export rate was explained by a lower carbon allocation to starch in relation to the decrease of k_{a1} (Fig. 2, Table 1).

Upon transfer to high light, the starch accumulation rate increased to three times the control value (Fig. 3). Starch content at the end of night progressively increased for three days after light change which indicated insufficient night mobilization. Carbon input and sucrose pool sizes doubled on the first day, then sucrose further increased for the two following days. Sucrose export increased but a lower portion of carbon input, relative to control, was mobilized (70% of the photosynthetic rate) and the export coefficient (k_{02}) was decreased by 25% (Table 1). This lower relative export was explained by a higher carbon allocation to starch as shown by an higher k_{a1} value (Fig. 3, Table 1).

Table 1. Comparison in different light conditions of parameters for input , distribution and export of carbon in a fourth mature leaf of maize plants analysed by a four compartmental model. Only results obtained on the first day after treatment are shown. Each value was expressed relative to control (mean of 11 or 12 repetitions). Absolute values are given in parenthesis.

		Light Conditions (µmol. photon m^{-2} s^{-1})		
		Low light (60)	Control (300)	High light (700)
Net Photosynthesis (µmol CO_2 m^{-2} s^{-1})		0.20	1.00 (16)	1.75
Transfer Coefficient (μs^{-1})	kal	0.54	1.00 (432)	1.60
	kø2	0.86	1.00 (732)	0.75
Sucrose Pools (μcm^{-2})	(Q2+Q3)	0.21	1.00 (89)	1.97
Starch Accumulation Rate (ng cm^{-2} s^{-1})		0.10	1.00 (6.7)	3.40
Fluxes (% P.N.)	Starch	8.00	16.00	30.00
	Export	92.00	84.00	70.00

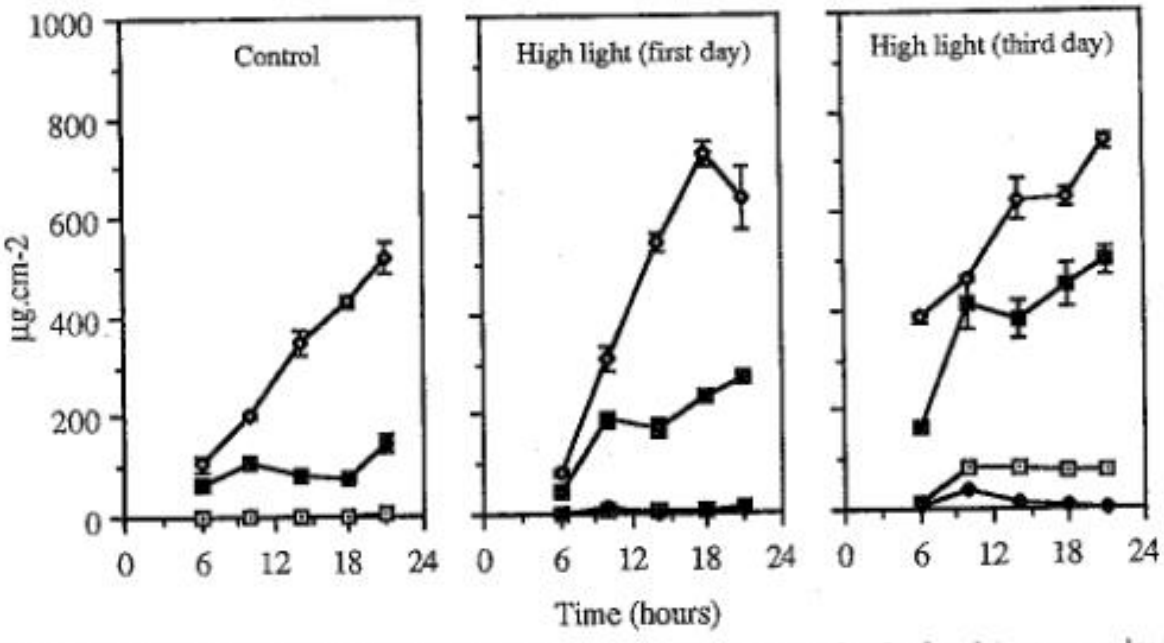


Fig. 3. Influence of a change in fluence rate on the main carbohydrate pools of a fourth mature maize leaf of plants transferred from 300 µmol photon $m^{-2}s^{-1}$ (control) to 700 µmol photon $m^{-2}s^{-1}$ (high light). Mean ± SE from three repetitions. Error bars smaller than symbols are not shown. Fructose (◆); Glucose (▣); Sucrose (■); Starch (◊).

4. Discussion and Conclusion

The compartmental analysis used to study partitioning and transfer of carbon between carbohydrate pools and export is of considerable value in terms of understanding how a source leaf regulates its newly assimilated carbon. However, steady state concentrations for sucrose are a prerequesite for a correct analysis (13). This point was verified from biochemical measurements (Figs 2, 3). The diurnal allocation pattern of carbon to starch was steady whatever the light control conditions. Sucrose content doubled within two hours and then remained constant throughtout the light period. This pattern was broadly found without alteration for the three days of experiment transfer to low or high light intensity (Figs 2, 3). Thus, sucrose concentration may be assumed to be rather constant during the chase period. A theoretical analysis of the stability of parameter estimation from the model showed that it was not very influenced by some variation in sucrose pool size at the end of the light period (JP Rocher, unpublished results).

Transfer to low light irradiance resulted in a decrease in net photosynthetic rate and in a lower translocation rate (Table 1). The reduction in the export flux was not proportional to the decrease in the photosynthetic rate. This seems to indicate that a minimum of carbon export was of prime importance for the source leaf. Similar results were reported by Servaites and Geiger (15) on sugar beet, Ho (7) on tomato, and Robbins and Pharr (12) on cucumber. Consequently, sucrose was rapidly turning over because most of the sucrose produced was translocated (92%, see Table 1) and export was probably partly maintained by the remobilization of previously stored sucrose and hexoses and from breakdown of starch. This leads to very low sucrose and starch pools at the end of the night (Fig. 2). During the following days the same pattern was found and probably implied a drastic decrease of nighttime export due to the very low reserve at the beginning of the night. The decline in carbon export and low storage observed under low light conditions coincided with a decrease in plant dry weight (P Maillard & JP Rocher, unpublished results).

Transfer to high light intensity caused an increase of net carbon assimilation and a strong increase of carbohydrate and export pools. (Table 1, Fig. 3). Mullen and Koller (10) also showed that daytime export rate in soybean leaves increased under higher photosynthetic photon flux density. However, in comparison with the increase of carbon assimilation in the leaf, carbon export seemed buffered and a slight decrease of the export transfer coefficient (k_{02}) was noted. Actually, mechanisms by which the source leaf controls allocation of carbon between export and storage leaf pools remains unclear. Our results in high light indicated that carbon export from the leaf was not directly related with the increase of total sucrose content in the leaf and suggested that sucrose concentration was only one of the parameters which could control export. The sucrose accumulation, also reported in several plants, suggests export limitation throught a limited loading capacity, a requirement for starch storage, or a limited sink demand for assimilates (5, 6, 8). The limiting export favoured reserve formation by allocation of an important part of newly fixed carbon (30%) to starch reserves. Starch accumulation rate increased over three times on the first day after transfer (Table 1). Our results suggested that export capacity of the leaf was limited also during the night following the first high light period, since about 60% of the starch and sucrose present at the end of the first day remained in the leaf at the beginning of the third photoperiod (Fig. 3). On the third day carbohydrate distribution between sucrose and starch was different from the first day under high light. Starch accumulated at a lower rate (close to control),

reaching the same final value as on the first day. Excess carbon appeared to be allocated to the sucrose pools. Concomitantly, both glucose and fructose content notably increased, suggesting starch degradation during the day (Fig. 3).

This study showed that a maize source leaf is adapted to maintain a relatively stable export of carbohydrates throughout the day, and from day to day, in spite of marked changes in carbon assimilation due to variations in light conditions. Both buffering of export rate and differences in carbon assimilation in response to changing light conditions altered the mode of regulation controlling sucrose and starch synthesis to create a new equilibrium between carbon partitioning, storage and export.

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Transport libérien et compartimentation des produits de la photosynthèse Données récentes

EDITORS

JEAN LOUIS BONNEMAIN, SERGE DELROT, WILLIAM J. LUCAS, JACK DAINTY

This book is an attempt to give a picture of the present state of research on phloem transport and assimilate partitioning. It is devoted to expert accounts of various aspects of the control of allocation, on ultrastructure and biology of specialized cells, on plasmodesmata, phloem-xylem exchanges, membrane transport, on sink metabolism, water relations, xenobiotic transport and on techniques and modelling. The topics are discussed, and an integration attempted, from the structural, physiological, biochemical and molecular points of view. The authors also try and look into the future in their areas.

The book arose out of a meeting, the Fourth International Conference on Phloem Transport and Assimilate Compartmentation, held at the Cognac Conference Centre "La Salamandre", Charente, France from 19 to 24 August, 1990. The Cognac Conference had 254 participating scientists from 25 countries and, for the book, topics and authors were selected from the participants who gave, in total, 40 oral presentations and 162 posters.

L'objectif de cet ouvrage est de faire un bilan de l'état actuel des recherches consacrées au transport libérien et à la ventilation des produits de la photosynthèse. Il est consacré à des analyses d'experts portant sur le contrôle de la ventilation des produits de la photosynthèse, l'ultrastructure et la biologie des cellules spécialisées, les échanges phloème-xylème, les plasmodesmes, les transports membranaires, le métabolisme des organes receveurs, les relations hydriques, les techniques et la modélisation, enfin le transport des xénobiontes. Ces différents sujets ont été développés et discutés en intégrant leurs aspects structuraux, physiologiques, biologiques et moléculaires. Les auteurs ont, par ailleurs, dressé des perspectives de recherche pour le futur.

L'ouvrage émane du IVe Congrès international sur le transport libérien et la compartimentation des assimilats qui s'est tenu à Cognac, France, du 19 au 24 août 1990. Ce congrès a rassemblé 254 scientifiques provenant de 25 pays. Les 44 chapitres du livre ont été sélectionnés à partir des 40 conférences et des 162 posters présentés lors de cette manifestation.

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