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

Pascale Maillard, Jean-Paul Rocher

To cite this version:

Pascale Maillard, Jean-Paul Rocher. Effect of light on the regulation of carbon partitioning in mature leaves of Zea mays L.. Recent advances in phloem transport and assimilate compartmentation. Ed. J.L. Bonnemain, S. Delrot, W.J. Lucas and J. Dainty, Ouest Editions, Presses Académiques, 27-32., 1991, 2908261618. hal-02930742

HAL Id: hal-02930742
https://hal.inrae.fr/hal-02930742

Submitted on 8 Oct 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

RECENT ADVANCES IN PHLOEM TRANSPORT AND ASSIMILATE COMPARTMENTATION

Transport libérien et compartimentation des produits de la photosynthèse Données récentes

EDITORS

Jean Louis Bonnemain
Serge Delrot
William J. Lucas
Jack Dainty

OUEST EDITIONS
Presses Académiques

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).

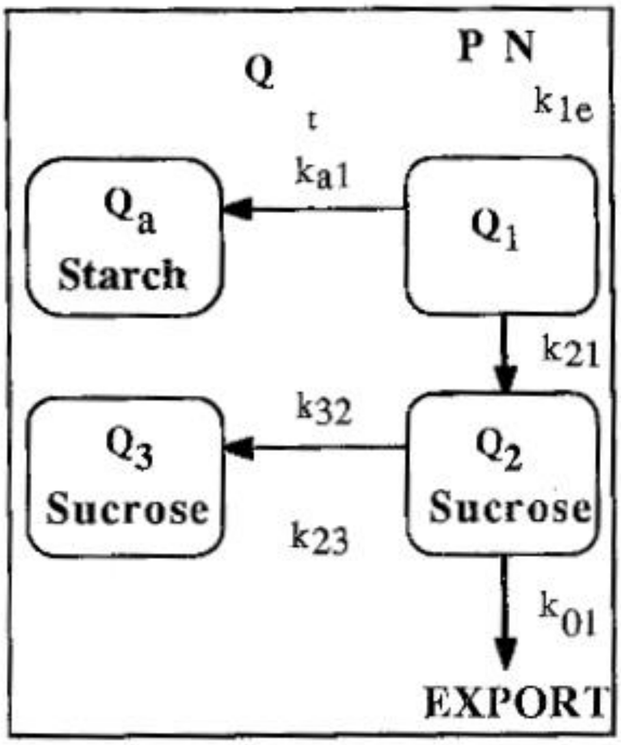

Fig. 1. Improved four compartment model for carbon distribution and export in a maize source leaf derived from the model described in Rocher and Prioul (13). PN = net photosynthesis; Q = pulse labelling; t = pulse duration; Q_1, Q_2, Q_3 = compartment sizes in mmol C $^{m-2}$.; Q_a = starch pool; k_{ij}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

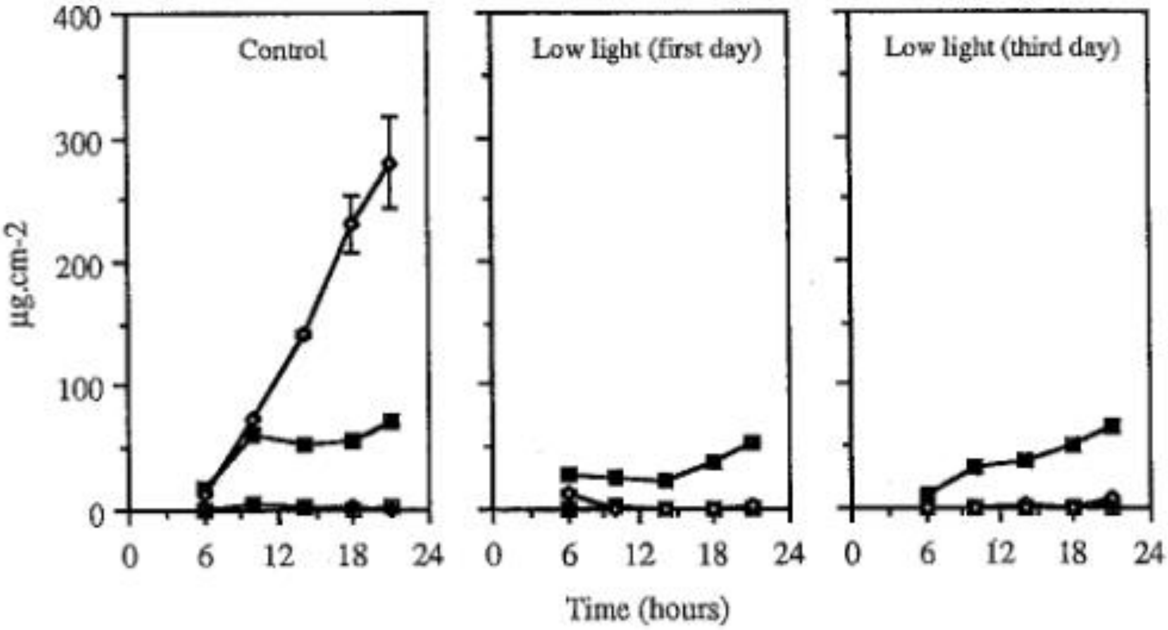

Fig. 2. Changes in the main carbohydrate pools of a fourth mature maize leaf of plants transferred from 300 µmol.photon $m^{-2}s^{-1}$ (control) to 60 µmol. photon $m^{-2}s^{-1}$ (low light) for three days. Mean ± SE from three repetitions. Error bars smaller than symbols are not shown. Fructose (◆); 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 (μ s^{-1})	kal	0.54	1.00 (432)	1.60
	kø2	0.86	1.00 (732)	0.75
Sucrose Pools (μ cm^{-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

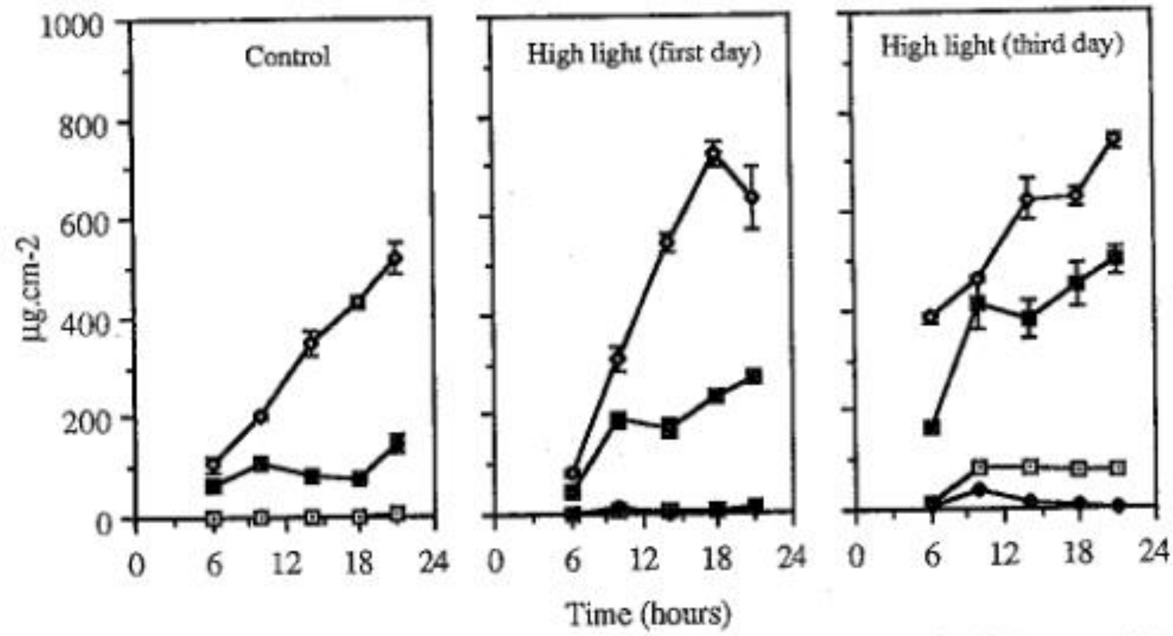

Fig. 3. Influence of a change in fluence rate on the main carbohydrate pools of a fourth mature maize leaf of plants transferred from 300 μmol photon $m^{-2}s^{-1}$ (control) to 700 μmol photon $m^{-2}s^{-1}$ (high light). Mean ± SE from three repetitions. Error bars smaller than symbols are not shown.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

5. Literature Cited

1. **Bergmeyer HU, Bernst E,** (1974) Sucrose. *In* Methods of enzymatic analysis (H.U. Bergmeyer, ed.), Vol. 3, pp. 1176-1179. Academic press, New York. ISBN 0-12-091303-8
2. **Dickson RE, Larson PR,** (1975) Incorporation of ^{14}C-photosynthetate into major chemical fractions of source and sink leaves of cottonwood. Plant Physiol **56**: 185-193
3. **Fondy BR, Geiger DR,** (1982) Diurnal pattern of translocation and carbohydrate metabolism in source leaves of *Beta vulgaris* L.. Plant Physiol **70**: 671-676
4. **Fondy BR, Geiger DR, Servaites JC** (1989) Photosynthesis, carbohydrate metabolism, and export in *Beta vulgaris* L. and *Phaseolus vulgaris* L. during square and sinusoidal light regimes. Plant Physiol **89**: 396-402
5. **Grange RI** (1985) Carbon partitioning and export in mature leaves of pepper (*Capsicum annuum*). J. Exp. Bot **36**: 734-744
6. **Grange RI** (1987) Carbon partitioning in mature leaves of pepper: Effects of transfer to high or low irradiance. J Exp Bot **38**: 77-83
7. **Ho LC** (1976) The relationship between the rates of carbon transport and of photosynthesis in tomato leaves. J Exp Bot **27**: 87-97
8. **Ho LC, Shaw AF, Hammond JBW, Burton KS** (1983) Source-sink relationships and carbon metabolism in tomato leaves.1. ^{14}C assimilate compartmentation. Ann Bot **52**: 365-372
9 **Moorby J, Jarman PD** (1975) The use of compartimental analysis in the study of the movement of carbon through leaves. Planta **122**: 155-168
10. **Mullen JA, Koller HR** (1988) Daytime and nighttime carbon balance and assimilate export in soybean leaves at different photon flux densities. Plant Physiol **86**: 880-884
11. **Prioul JL, Rocher JP** (1985) Interaction between source and sink, between sources and between sinks. *In* Photosynthesis and Physiology of the whole plant. Organisation for Economic Cooperation and Developpement ed., Paris, pp 56-84
12. **Robbins NS, Pharr DM** (1987) Regulation of photosynthetic carbon metabolism in cucumber by light intensity and photosynthetic period. Plant Physiol **85**: 592-597
13. **Rocher JP, Prioul JL** (1987) Compartmental analysis of assimilate export in a mature maize leaf. Plant Physiol Biochem **25**: 531-540
14. **Rocher JP** (1988) Comparison of carbohydrate compartmentation in relation to photosynthesis assimilate export and growth in a range of maize genotypes. Aust J Plant Physiol **15**: 677-686
15. **Servaites JC, Geiger DR** (1974) Effects of light intensity and oxygen on photosynthesis and translocation in sugar beet. Plant Physiol **54**: 575-578

Adress all inquiries to the Publisher
Ouest Editions, case postale 5001, 44086 Nantes Cedex 03, France
Phone (33) 40 93 03 98. Fax (33) 40 93 98 21

Copyright 1991 OUEST EDITIONS

Printed in France

Under the conditions stated below the owner of copyright for this book grants permission to users to make photocopy reproductions of any part of its contents for personal or internal organizational use, or for personal or internal use of specific clients. This consent is given on the condition that the copier pay the stated per-copy fee through the Copyright Clearance Center, Inc., 27 Congress Str., Salem, MA O1970, as listed in the most current issue of "Permissions to Photocopy" (Publisher's Fee List,distributed by C.C.C.), for copying beyond that permitted by sections 107 or 108 of the US Copyright Law. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for release.

Exception : the only editors and authors of this book stay free for reproducing or publishing, partly or entirely, their only own contribution, this under reserve of mentioning the references of the original publication.

In a general way, all rights are reserved for all countries, whatever the kind of support of publication.

Library of Congress Cataloging-in-Publication Data

International Conference on Phloem Transport (4th : august 19-24, 1990, hold in Cognac, France)
Phloem transport : proceedings of an International Conference on Phloem Transport and assimilate compartmentation.
The book includes bibliographical references and index.
I) Control of allocation and partitioning. II) Ultrastructure and biology of specialized cells. III) Phloem-Xylem exchanges. IV) Plasmodesmata. V) Membranes in relation to loading and unloading. VI) Sink metabolism. VII) Water relations and sink function. VIII) Techniques and Modeling. IX) Xenobiotic transport.

ISBN 2 908261 61 8

RECENT ADVANCES IN PHLOEM TRANSPORT AND ASSIMILATE COMPARTMENTATION

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.

9 782908 261615

prix/price

400 F

80 US $

Ouvrage publié avec l'aide du Ministère de la Recherche et de la Technologie (DIST)

OUEST EDITIONS
Presses Académiques