

Applied
Botany
Series

Volume 2

Crop Processes in Controlled Environments

edited by
A. R. Rees
K. E. Cockshull
D. W. Hand
and R. G. Hurd



CROP PROCESSES IN CONTROLLED ENVIRONMENTS

*Proceedings of an International Symposium
held at the Glasshouse Crops Research Institute,
Littlehampton, Sussex, England, July 1971*

Edited by

A. R. REES, K. E. COCKSHULL,
D. W. HAND *and* R. G. HURD

1972



ACADEMIC PRESS - London and New York

ACADEMIC PRESS INC. (LONDON) LTD

24-28 Oval Road

London NW1

United States Edition published by

ACADEMIC PRESS INC.

111 Fifth Avenue

New York, New York 10003

Copyright © 1972 by

ACADEMIC PRESS INC. (LONDON) LTD

All Rights Reserved

No part of this book may be reproduced in any form by photostat, microfilm, or any other means without written permission from the publishers

Library of Congress Catalog Card Number: 72-8445

ISBN: 0-12-585440-4

Printed in Great Britain by

Butler & Tanner Ltd, Frome and London

Preface

In recent years considerable attention has been given to studies of plants and crops in relation to their environment. Progress has been made both in controlling the plant environment and in improving the efficiency of agricultural and horticultural practice. Most factors of the glasshouse environment can be modified or controlled, but there is still uncertainty in many cases about the optimum conditions for plant growth and crop production and there is little information available about the effects of short-term deviations from the optimum on plant behaviour. As one speaker commented, the plant in its natural environment proceeds from crisis to crisis, and the grower attempts to reduce the frequency and extent of these crises.

It was the aim of the Symposium to explore recent advances in several technical and scientific fields of research on crop and plant processes with the object of revealing areas where further research is most urgently required. These include:

1. Recent developments in glasshouse technology, such as light-modulated control of temperature and carbon dioxide concentration; supplementary lighting; growing rooms; plastic houses and mini-glasshouses.
2. Micrometeorological and physical methods, increasingly used in studying field crops, which have as yet been little used in the glasshouse environment where many of the determining factors can be better controlled.
3. New developments in controlled-environment cabinets which allow precise gas-exchange studies, the independent control of root and shoot temperatures, and the use of natural light or improved artificial sources.
4. Advances in some areas of plant physiology of especial relevance to crop production including photorespiration; the biochemical control of photosynthesis; translocation and the control of accumulation of assimilates; hormonal control of growth and development.
5. The extension of computer simulation and quantitative analysis to crop processes hitherto treated descriptively.

The Symposium was conceived and largely organized by Dr J. Warren Wilson to mark the formal opening of the new Plant Physiology buildings and controlled-environment facilities on 14 July 1971 by the Rt Hon. Mrs Margaret Thatcher, M.P., Secretary of State for Education and Science. We are grateful to the Governing Body of the G.C.R.I., who underwrote the costs of the Symposium, and to the Trustees of the Underwood Fund for providing financial support to enable the organizers to invite overseas speakers. Many members of the Institute staff helped to organize the Symposium, and we should like to thank them all for their efforts. We are particularly grateful to the authors of the papers and to the session chairmen. Permission to reproduce tables and figures is acknowledged in the respective captions.

June 1972

A. R. REES
K. E. COCKSHULL
D. W. HAND
R. G. HURD

Contents

Preface	ix
-------------------	----

Introductions

1. Controlled environments	
D. RUDD-JONES	1
2. Control of crop processes	
J. WARREN WILSON	7

Section I Controlled Environments

Chairman: Dr D. Rudd-Jones

I.1. Phytotrons: past achievements and future needs	
J. P. NITSCH†	33
I.2. Future trends in structures for protected cropping	
G. F. SHEARD	57
I.3. Principles and progress in environmental control systems	
G. E. BOWMAN	63
I.4. Analysis of the microclimate in the glasshouse	
S. W. BURRAGE	79
I.5. A prototype, airtight, daylit, controlled environment cabinet and the rationale of its specification	
B. ACOCK	91

Section II Environment-Crop Relations

Chairman: Professor J. L. Monteith

II.1. Introduction: some partisan remarks on the virtues of field experiments and physical analogues	
J. L. MONTEITH	107
II.2. Transport of nutrients from soil to crops	
R. SCOTT RUSSELL	111

† Deceased.

II.3. Responses of the barley crop to soil water stress	
O. RACKHAM	127
II.4. Gas exchange of field crops	
J. V. LAKE	139
II.5. Micro-environment, carbon dioxide exchange and growth in grass swards	
E. L. LEAFE	157
II.6. The relationship between crop physiology and analytical plant physiology	
C. P. WHITTINGHAM	175
II.7. Crop processes and physics	
P. D. JARMAN	185

Section III Environment-Plant Relations

Chairman: Professor W. W. Schwabe

III.1. Environment-plant relations: introduction	
W. W. SCHWABE	197
III.2. Net assimilation of plants as influenced by light and carbon dioxide	
P. CHARTIER	203
III.3. The response of the potato plant and tuber to temperature	
W. G. BURTON	217
III.4. Photoperiodic control of flowering in the chrysanthemum	
K. E. COCKSHULL	235
III.5. Hormonal mediation of plant responses to the environment	
D. J. OSBORNE	251
III.6. The control of the rate and direction of phloem transport	
A. J. PEEL	265

Section IV Internal control mechanisms

Chairman: Professor J. F. Sutcliffe

IV.1. Internal control mechanisms: introduction	
J. F. SUTCLIFFE	281
IV.2. Biochemical limitations to photosynthetic rates	
K. J. TREHARNE	285
IV.3. The relationship between photosynthesis and respiration	
L. J. LUDWIG	305
IV.4. Respiration and growth	
F. W. T. PENNING DE VRIES	327

IV.5. Physiological and biochemical responses to wilting and other stress conditions

S. T. C. WRIGHT 349

Conclusion

Some further aspects of control of crop processes

P. F. WAREING 363

Author index 373

Subject index 383

Introduction 1

Controlled environments

D. RUDD-JONES

Glasshouse Crops Research Institute, Littlehampton, Sussex, England

The scientist working in controlled environments has unique opportunities to determine the precise limits of productivity of plants. If he is working also in the interests of the glasshouse industry he is in the fortunate position that his "laboratory" is also what might be termed his "production unit"—a concept which embraces the whole plant or crop in the environment in which it is growing. The more closely the glasshouse can be made to simulate the controlled environment cabinet, the nearer it should be possible to get to maximum productivity in commercial crops. It is now accepted that yields of tomatoes in excess of $250 \times 10^3 \text{ kg ha}^{-1}$ and cucumbers in excess of $375 \times 10^3 \text{ kg ha}^{-1}$ can be achieved. This is five or six times the weight of apples that can be produced per unit area on a comparable dry weight basis, four or five times the weight of cereal grain, and twice the yield of potato tubers. In commercial practice full account has to be taken of the economics of crop production in controlled environments; the capital and running costs are high and become higher the more sophisticated the controls. One environmental factor only—solar radiation—is beyond the control of the scientist.

The development of experimental studies of the interactions of whole plants and crops with their environments under precisely controlled conditions has been comparatively recent. The main interests and the major advances in plant physiology in this country have been in two general areas; at the one extreme, field experiments with crops, and at the other, laboratory experiments with unicellular organisms, single cells, tissues or parts of plants.

The opening of the first Phytotron at Pasadena provided a great stimulus to plant physiologists to work in controlled environments with whole plants. Relatively unsophisticated cabinets had been used in this country

before the war (e.g., Stoughton, 1930; Wilson, 1937), but often for pathological rather than physiological research. This late development of research in controlled environments with whole plants is reflected by the long time lag in the exploitation of environmental control, and particularly carbon dioxide enrichment, to increase productivity in commercial practice. As early as 1916 in the Second Annual Report of the Experimental and Research Station at Cheshunt—the predecessor of the Glasshouse Crops Research Institute—an account (Lister, 1917) was given of the measurement of carbon dioxide in the glasshouse atmosphere which showed that it could reach four or five times the ambient concentration at soil level, whereas at the top of the house it was only just above ambient although during the night the concentration normally rose. Some of the first experiments to investigate the possibility of increasing yields in glasshouse crops by carbon dioxide enrichment were done at Cheshunt by Timmis (1923). These experiments involved the injection of carbon dioxide into the glasshouse in concentrations up to ten times ambient and they were continued at Cheshunt and in association with the Research Institute of Plant Physiology, Imperial College, London. Owen and Williams (1923) (the latter author was specially appointed for the carbon dioxide investigations), Owen *et al.* (1926) and Small and White (1930) demonstrated increased yields of tomatoes and cucumbers in glasshouses enriched with carbon dioxide from several different sources. Bolas and Henderson (1928) obtained increases in the vegetative growth of cucumbers and other plants under laboratory conditions using pure carbon dioxide and Bolas and Melville (1935) showed yield increases of tomatoes of nearly 14% over the whole cropping season from enrichment with carbon dioxide produced by burning paraffin.

Experiments at the two Institutes continued up until the war. There was then a long gap until the 50s and early 60s when there were reports of increased yields of cucumbers, tomatoes and heated lettuce from several European countries (Kilbinger, 1951; Klougart, 1963, 1964) and North America (Wittwer and Robb, 1964). In Holland, Gaastra (1959) published a detailed account of the more fundamental aspects and Briejër (1959) a more general account. The latter paper had the provocative title "An abandoned gold mine; the supplementary application of carbon dioxide". In this country Gardner (1963, 1964) demonstrated the value of carbon dioxide enrichment for heated lettuce and winter-flowering chrysanthemums at the Lee Valley Experimental Horticulture Station. The rapid developments in glasshouse engineering and control instrumentation that derived from the work of L. G. Morris and his colleagues at the National Institute of Agricultural Engineering pointed the way for much more precise and integrated control of environmental factors including carbon

dioxide. This led to the experiments in the so-called "cuvette" glasshouse by Lake (1966) who suggested that ultimately the control of the glasshouse environment might be achieved by a system operated by a digital computer. This work was paralleled at the Glasshouse Crops Research Institute by the development of the Multifactorial Glasshouse Unit in which Cooper *et al.* (1966), Calvert (1968) and Calvert and Slack (1970) have done critical experiments on the integrated control of temperature, ventilation and carbon dioxide.

Thus it has taken nearly forty years to exploit commercially the original observations of the advantages of carbon dioxide enrichment. This has been due in large part to the fact that enrichment did not become practically feasible until systems of automatic control of temperature and ventilation were generally available, and even today only about a third of the heated tomato acreage in the U.K. is carbon dioxide-enriched, although probably nearly all the early crop, which shows the greatest benefit, is treated.

By contrast with the slow development of research on the interaction of crops grown in controlled conditions with their environments, there has been a much more rapid adoption by commercial growers of growth-regulating chemicals. Although these studies stem from more fundamental work by physiologists such as Went (1957), Hendricks (1967) and Cathey (1967), it was the essentially empirical approach of Preston and Link (1958), Tolbert (1960), Riddell *et al.* (1962), Tso (1964) and Cathey *et al.* (1966) that led to the dramatic developments in the control of flowering which have now become widely adopted in commercial practice.

At the present time the practical methods of controlling daylength for chrysanthemums which have been developed scientifically are being widely used in conjunction with growth retardants. Recently, too, research on supplementary illumination of chrysanthemums undertaken at the A.R.C. Unit of Flower Crop Physiology (Cockshull and Hughes, 1968) in controlled environments has led to recommendations for commercial use which are being taken up by some growers.

The next stage must be to achieve an understanding of the mode of action of synthetic growth-regulating chemicals and of their interactions with environmental factors and with internal control mechanisms involving naturally-occurring growth hormones. At the same time there is a need to study the more fundamental aspects of photoperiodism including the role of phytochrome (Borthwick, 1964), the pigment that mediates the developmental effects of light; the possible existence of a flowering hormone should also be investigated. This could lead to a further exploitation of the glasshouse environment for increased productivity and improved quality and to a better understanding of the genetical control of physiological

characters that could be turned to advantage by the breeding of varieties for particular cultural systems. This in turn might stimulate a more rational and critical examination of alternative, cheaper systems of protecting crops and of extending the variety of such crops.

The declared object of the Symposium is "to evaluate recent advances in several technical and scientific fields which have important implications for research on crop and plant processes, and to suggest areas where further research is most urgently required". It comes at an especially opportune time for the Glasshouse Crops Research Institute. The Plant Physiology Department has, over the past four years, expanded both in staff and facilities for research on environmental control, on photoperiodism and on other crop processes. There would appear to be a need now to integrate the environmental control work with developmental studies.

After a decade of intensive research with whole plants in controlled environments, in which the controls have become more and more precise, physiologists are now returning to chemical and physical studies at the cell level with plant tissues or parts of plants in parallel with the whole plant studies. This more analytical approach which is necessary in order to acquire basic information on crop processes will then have to be correlated with data on whole plants.

The organizers have attempted to provide for the consideration in logical sequence of these changing trends by arranging the Symposium in four sessions. The opening session is devoted to a consideration of controlled environment facilities, the associated instrumentation, monitoring and control of the glasshouse environment, and future trends in structures and materials for protected cropping. The sessions which follow are concerned with the environment-crop and environment-plant relations and with internal control mechanisms.

References

- BOLAS, B. D. and HENDERSON, F. Y. (1928). Effect of increased carbon dioxide on the growth of plants. *Ann. Bot. O.S.* **42**, 509-523.
- BOLAS, B. D. and MELVILLE, R. (1935). The effect on the tomato plant of carbon dioxide produced by combustion. *Ann. appl. Biol.* **22**, 1-15.
- BORTHWICK, H. A. (1964). Control of photomorphogenesis by phytochrome. *Abstr. Pap. 10th Int. bot. Congr., Edinburgh, 1964*, 197.
- BRIEJÈR, C. V. (1959). Een verlaten goudmijn: koolzuurbemesting. *Meded. Dir. Tuinb.* **22**, 670-674.
- CALVERT, A. (1968). Effects of temperature on cropping of glasshouse tomatoes. *Rep. Glasshouse Crops Res. Inst.* 1967, 52.
- CALVERT, A. and SLACK, G. (1970). Effects of carbon dioxide concentration on glasshouse tomatoes. *Rep. Glasshouse Crops Res. Inst.* 1969, 61-62.

- CATHEY, H. M. (1967). Photobiology in horticulture. *Proc. 17th Int. hort. Congr., 1966* **3**, 385-391.
- CATHEY, H. M., STEFFENS, G. L., STUART, N. W. and ZIMMERMAN, R. H. (1966). Chemical pruning of plants. *Science, N.Y.* **153**, 1382-1383.
- COCKSHULL, K. E. and HUGHES, A. P. (1968). First two weeks of short-day treatment are critical with chrysanthemum. *Grower* **70**, 520-521.
- COOPER, A. J., HURD, R. G. and GISBORNE, J. H. (1966). The effect of ventilating the control glasshouses in CO₂ enrichment comparisons. *Rep. Glasshouse Crops Res. Inst. 1965*, 142-144.
- GAASTRA, P. (1959). Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. *Meded. LandbHoogesch. Wageningen* **59**, (13), 1-68.
- GARDNER, R. (1963). Response differs with variety. *Grower* **59**, 813-814.
- GARDNER, R. (1964). CO₂ for glasshouse crops. *Agriculture, Lond.* **71**, 204-208.
- HENDRICKS, S. B. (1967). Photoreactions controlling plant growth. *Proc. 17th Int. hort. Congr., 1966* **3**, 381-384.
- KILBINGER, A. (1951). Die Dúngung mit Kohlensäure. *Technik Bauern Gärtn., G*, 10th October 1951; 542.
- KLOUGART, A. (1963). Agurkkulturens kuldioxydforsyning. *Gartner Tidende* **79**, 463-468.
- KLOUGART, A. (1964). Kuldioxyd-tilførsel i vintertiden virker vækstfremmende på salat. *Gartner Tidende* **80**, 18-20.
- LAKE, J. V. (1966). Measurement and control of the rate of carbon dioxide assimilation by glasshouse crops. *Nature, Lond.* **209**, 97-98.
- LISTER, A. B. (1917). Carbon dioxide control of greenhouse air. *Rep. exp. Res. Stn. Cheshunt, 1916*, 9.
- OWEN, O. and WILLIAMS, P. H. (1923). Carbon dioxide in relation to glasshouse crops. Part II. The preparation of an atmosphere rich in carbon dioxide. *Ann. appl. Biol.* **10**, 318-325.
- OWEN, O., SMALL, T. and WILLIAMS, P. H. (1926). Carbon dioxide in relation to glasshouse crops. Part III. The effect of enriched atmospheres on tomatoes and cucumbers. *Ann. appl. Biol.* **13**, 560-576.
- PRESTON, W. H. Jr. and LINK, C. B. (1958). Use of 2,4-dichlorobenzyltributyl phosphonium chloride to dwarf plants. *Pl. Physiol., Lancaster Suppl.* **33**, XLIX.
- RIDDELL, J. A., HAGEMAN, H. A., J'ANTHONY, C. M. and HUBBARD, W. L. (1962). Retardation of plant growth by a new group of chemicals. *Science, N.Y.* **136**, 391.
- SMALL, T. and WHITE, H. L. (1930). Carbon dioxide in relation to glasshouse crops. Part IV. The effect on tomatoes of an enriched atmosphere maintained by means of a stove. *Ann. appl. Biol.* **17**, 81-89.
- STOUGHTON, R. H. (1930). Apparatus for the growing of plants in a controlled environment. *Ann. appl. Biol.* **17**, 90-106.
- TIMMIS, L. B. (1923). Investigations upon the fertilising effects of carbon dioxide. *Rep. exp. Res. Stn Cheshunt, 1922*, 57-65.
- TOLBERT, N. E. (1960). (2-chloroethyl) trimethylammonium chloride and re-

- lated compounds as plant growth substances. II. Effect on growth of wheat. *Pl. Physiol., Lancaster*, **35**, 380-385.
- Tso, T. C. (1964). Plant growth inhibition by some fatty acids and their analogues. *Nature, Lond.* **202**, 511-512.
- WENT, F. W. (1957). "The experimental control of plant growth". Waltham, Mass.: Chronica Botanica.
- WILSON, A. R. (1937). Apparatus for growing plants under controlled environmental conditions. *Ann. appl. Biol.* **24**, 911-931.
- WITTWER, W. H. and ROBB, W. M. (1964). Carbon dioxide enrichment of greenhouse atmospheres for food crop production. *Econ. Bot.* **18**, 34-56.

Introduction 2

Control of crop processes

J. WARREN WILSON

Glasshouse Crops Research Institute, Littlehampton, Sussex, England

I. Control of glasshouse crop production

A. Environmental control in the glasshouse

The annual yield of glasshouse crops is roughly three times that of field crops, expressed as dry matter per unit area of land (Table I). The contrast is greater for fresh weight yields, since glasshouse products tend to have

Table I

Yields, values and water contents for some crops in the United Kingdom

	<i>Yield as dry matter † (g m⁻² year⁻¹)</i>	<i>Value per unit dry weight (pence g⁻¹)</i>	<i>Water content per unit dry weight (g g⁻¹)</i>
Field crops			
Wheat (grain)	400	0.003	0.1
Sugar beet (sugar)	600	0.004	0.0
Potato (tuber)	700	0.01	3.0
Apple (fruit)	400	0.04	4.0
Protected crop			
Mushroom (fruiting body)	34,000	0.4	9.0
Glasshouse crops			
Tomato (fruit)	1100	0.5	19.0
Chrysanthemum (pot plant)	1800	0.6	6.0

higher water contents. The mushroom is somewhat comparable to glasshouse crops in being grown in a protected environment; its high yield per unit land area is partly due to the stacking of trays, often in four layers.

Whereas agricultural crops are grown mainly for their nutritional value, this is of little significance in glasshouse crops, which are grown largely for the attraction of their flavour and appearance. For these qualities, the consumer pays 10–100 times as much for glasshouse produce as for the produce of field crops in this country (dry matter basis).

These high values reflect the cost of providing a large measure of environmental control. Control of temperature, allowing year-round production of high value crops, is perhaps most important. In a modern glasshouse the control system can regulate temperature within $\pm 1^\circ\text{C}$ —except when ambient temperature is excessive—and the need for such precision is indicated by the estimate (Calvert, 1971) that a 1°C difference in mean temperature can alter net returns on a tomato crop by about 25 p m⁻² (£1000 per acre). Other factors which can be controlled in the glasshouse are:

(a) Carbon dioxide concentration: a level of about 2 g m⁻³ (three times ambient) is often used for glasshouse vegetables, and raises tomato yields by some 40% (Calvert and Slack, 1971).

(b) Water supply is independent of rainfall, and automatic irrigation can provide control of both water and nutrient supply; some control of atmospheric humidity is also possible.

(c) Daylength control, by artificial lighting and blackout covers, allows programmed production of photoperiodically sensitive crops.

More sophisticated light-dependent control systems are now available for regulating temperature, humidity and carbon dioxide concentration in relation to prevailing light (Bowman, 1972).

The degree of environmental control that is commercially worthwhile in the glasshouse depends on its cost, on the responses of the crop, and on an understanding of these responses without which optimal control settings are not known. The present need is for progress not in control engineering—efficient systems have been devised for controlling the glasshouse environment—but in crop science, since knowledge of crop responses to the various environmental factors is not yet adequate for informed commercial exploitation of the available environmental control systems.

B. Limitation of crop production by daylight

The major climatic factor not controlled in the glasshouse is light. At present supplementary artificial lighting costs too much to be commercially

worthwhile except in certain marginal cases, such as in propagation and in chrysanthemum flower production in midwinter (Canham *et al.*, 1969). Accordingly, since light is the source of energy and the ultimate limitati to crop yield, it is critically important to make efficient use of daylight falling on the glasshouse. Efficiency depends on glasshouse structure, setting of the glasshouse environment, cultural practice and genotype.

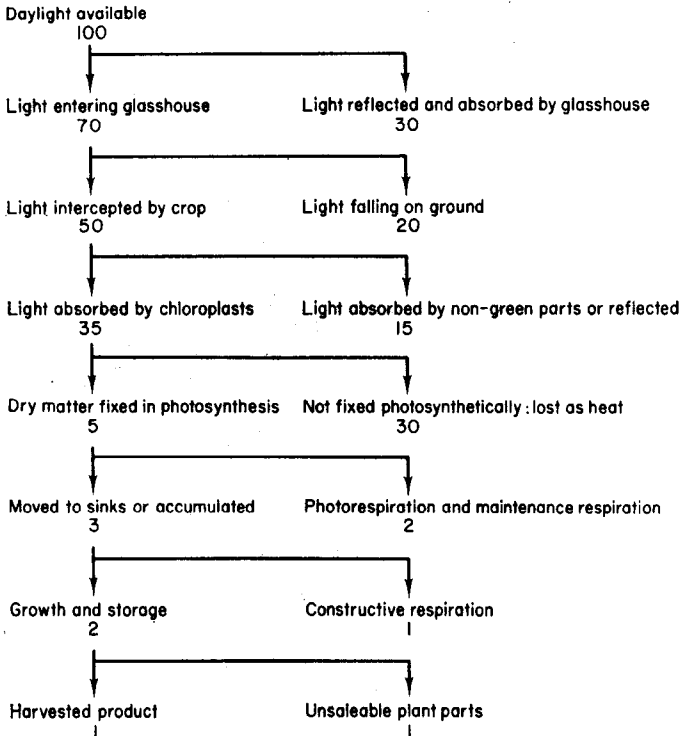


Fig. 1. Efficiency of use of photosynthetically-active light energy in annual production of harvestable dry matter by a glasshouse crop.

At present, glasshouse crops seldom achieve more than 1% efficiency in using light energy for the production of the energy-rich plant material that is harvested. Substantial losses occur at various stages in the process, as roughly indicated in Fig. 1. It is the task of the crop scientist to identify limiting or controlling factors at each stage and, through an understanding of the control of the chain of processes, to find ways of relieving limitations and increasing efficiency.