Published 1994

Physiology and Determination of Crop Yield

Related Society Publications

Crop Quality, Storage, and Utilization

Limitations to Efficient Water Use in Crop Production

Nitrogen in Crop Production

Physiological Aspects of Crop Yield

Physiological Aspects of Crop Growth and Development

Roots, Nutrient and Water Influx, and Plant Growth

For more information on these titles, please contact the ASA, CSSA, SSSA Headquarters Office; Attn: Marketing; 677 South Segoe Road; Madison, WI 53711-1086. Phone: (608) 273-8080 ext. 322. Fax: (608) 273-2021.

Physiology and Determination of Crop Yield

Editors
K. J. Boote, J. M. Bennett, T. R. Sinclair, and G. M. Paulsen

Based on the proceedings of an international symposium sponsored by ASA, CSSA, SSSA, USDA-ARS, and the University of Florida Institute of Food and Agricultural Sciences, and held at the University of Florida, Gainesville, Florida, 10–14 June 1991.

American Society of Agronomy, Inc.
Crop Science Society of America, Inc.
Soil Science Society of America, Inc.
Madison, Wisconsin, USA

1994

Cover Design: Lyda Toy
Cover Artwork: Lyda Toy

Library of Congress Cataloging-in-Publication Data

Physiology and determination of crop yield / editors, K.J. Boote ... [et al.].
p. cm.
"Based on the proceedings of an international symposium sponsored by ASA ... [et al.] and held at the University of Florida, Gainesville, Florida, 10–14 June 1991."
Includes bibliographical references.
ISBN 0-89118-122-9
1. Crops—Physiology—Congresses. 2. Crop yields—Congresses. I. Boote, K. J. II. American Society of Agronomy. III. Crop Science Society of America. IV. Soil Science Society of America.
SB112.5.P49 1994
581.1—dc20 94-12436
CIP

Printed in the United States of America

CONTENTS

Metabolism

Environmental Stresses

FOREWORD

Physiology is the science of biological processes and functions. Plant physiology had its roots in the early work of Joseph Priestley in 1772 who demonstrated plants give off O_2 in the process of photosynthesis but he did not understand that process. Robert Mayer, a German scientist, pointed out in 1845 the significance of C fixation via photosynthesis to the biological world. The world depends on green plants to convert solar energy into organic matter.

Crop physiology, as the basis of understanding crop growth, development, and management, emerged in the 1950s and 1960s replacing the empirical approaches to crop management of previous decades. The CSSA published a landmark volume on crop physiology as a product of an international symposium held at the University of Nebraska in 1969. Knowledge of plant processes and controlling mechanisms increased dramatically during the intervening 24 years since that symposium and it was appropriate to revisit this topic. Hence a symposium was hosted by the University of Florida at Gainesville in 1991. We congratulate the planners and authors from the USA and throughout the world for sharing their authoritative synthesis and views on this intricate topic. The authors have clarified and added detail and insights about crop growth and development, metabolism, and environmental stresses. The advancement of knowledge recorded in this book reflect, in part, the capacity of crop and soil scientists to address expanding concerns of society about the environment and the impact of human activity on our food and fiber production capacity.

This book will enable teachers, researchers, and practitioners to raise new questions, to prepare new knowledge and understanding and to develop appropriate techniques and solutions to ensure an abundant food and fiber supply while protecting our natural resources. To the organizers, editors, and authors we are indebted and share in their pride of a job well done.

CALVIN D. QUALSET, *president*
American Society of Agronomy

VERNON B. CARDWELL, *president*
Crop Science Society of America

LARRY P. WILDING, *president*
Soil Science Society of America

PREFACE

The international symposium, "Physiology and Determination of Crop Yield," was held 10–14 June 1991 at the University Centre Hotel, Gainesville, Florida. The Symposium was cosponsored by ASA, CSSA, and SSSA, and was cohosted by the University of Florida/Institute of Food and Agricultural Sciences and the USDA-ARS.

Twenty-five years have passed since the successful 1969 symposium at Lincoln, Nebraska, and resulting book entitled *Physiological Aspects of Crop Yield*. Scientific knowledge and understanding of physiological and genetic factors influencing crop yield have advanced considerably during that period, aided in part by increased numbers of researchers, new techniques, and new instrumentation. Thus, the goal of the 1991 symposium was to review the scientific advances since 1969, and to integrate the current understanding of physiological processes that influence crop growth and yield.

At the 1969 symposium, there prevailed a sense of urgency in increasing world food production to feed a rapidly expanding world population as well as an optimism that many future breakthroughs in crop production were possible. The success of the "Green Revolution" dominated the 1969 symposium presentations of genetic and cultural advances to improve production. Between 1969 and the present, the world population has continued to grow and food production has essentially kept pace with population growth, although food distribution remains problematic. While yield potential has continued to rise, optimism is no longer unbounded that it can increase indefinitely. Opinion is mixed on this point: some plant breeders point to the steady rate of genetic gain and propose that this will continue into the future, while others warn that crop yields may be approaching potential limits, limits imposed by light, temperature, water, and season.

Knowledge and understanding of crop growth processes, particularly relative to root, leaf, and seed growth, has increased considerably since 1969. Advances in our insight into metabolic processes have been dramatic, especially for photosynthesis and N_2 fixation. The first hints of the C_4 photosynthetic pathway were barely comprehended in 1969, but by 1976 whole books were available to explain the new C_4 pathway relative to the C_3 pathway. Likewise, the O_2-fixing behavior of ribulose-1,5 bisphosphate carboxylase-oxygenase was only conclusively resolved by 1971, but has now been thoroughly published in physiology texts. Rather than merely review already well-published photosynthetic pathways, symposium program planners chose to emphasize the regulation and integration of biochemical processes related to photosynthesis, N_2 fixation, C metabolism, N metabolism, nutrient uptake, and organ growth.

Environmental stresses, some natural and some man-induced, have become more important limitations to global food production than are inherent physiological limitations. These environmental challenges include: air pollutants, ultraviolet radiation, elevated CO_2 concentration, elevated temperature, drought, and low temperature. Crop responses to climate change, air pollution and ultraviolet irradiance were highlighted in this symposium because of their possible impacts on food security and the need to minimize effects of human activities on our environment.

The proposal for the 1991 symposium and book was initiated by T.J. Gerik and K.J. Boote in March 1989 to follow the 1969 symposium and to update the 1969 book with the current state of scientific knowledge. An ad hoc committee of R.M. Shibles (chair), K.J. Boote, J.D. Eastin, R.A. Fischer, T.J. Gerik, D.J. Hume, W.R. Jordan, D.P. Knievel, B. Larkins, R.S. Loomis, B.A. Martin, C.J. Nelson, and L.E. Schrader was appointed to recommend to the CSSA board the possible symposium sites, sponsors, funding sources, and potential topics. The Program Steering Committee [K.J. Boote and T.R. Sinclair (cochairs), S.A. Barber, T.J. Gerik, D.J. Hume, D.P. Knievel, J.M. Norman, and R.M. Shibles] was appointed 13 March 1990 by CSSA President Steve A. Eberhart to plan the program for an international symposium on "Physiology and Determination of Crop Yield." Local arrangements were handled by T.R. Sinclair, K.J. Boote, and J.M. Bennett.

We express our appreciation to the 210 participants of the symposium, session chairs (D.P. Knievel, D.J. Hume, T.J. Gerik, and R.M. Shibles), speakers, discussants, poster presentors, and those assisting with local arrangements. The symposium and invited speakers were generously supported by ASA, CSSA, SSSA, University of Florida-IFAS (Institute of Food and Agricultural Sciences), USDA-ARS, LI-COR, Inc., Northrup-King Company, Inc., Pioneer Hi-Bred International, Inc., Stoller Chemical Company of Florida, Inc., DeKalb Plant Genetics Foundation, and U.S. Borax Research Corp.

K.J. Boote, *coeditor*
University of Florida
Gainesville, Florida

J.M. Bennett, *coeditor*
University of Florida
Gainesville, Florida

T.R. Sinclair, *coeditor*
USDA-ARS
University of Florida
Gainesville, Florida

G.M. Paulsen, *coeditor*
Kansas State University
Manhattan, Kansas

CONTRIBUTORS

S. L. Albrecht	Associate Scientist, Department of Agronomy, University of Florida, Gainesville, FL 32611-0840; present position and address is Microbiologist, USDA-ARS, Columbia Plateau Conservation Research Center, Pendleton, OR 97801.
Leon Hartwell Allen, Jr.	Soil Scientist, USDA-ARS, and Professor of Agronomy, University of Florida, Gainesville, FL 32611-0846.
Jeffrey S. Amthor	Environmental Scientist, Lawrence Livermore National Laboratory, Livermore, CA 94550.
Roger B. Austin	Institute for Plant Science Research, Cambridge, England; present position is Visiting Scientist at Estacion Experimental de Aula Dei, C.S.I.C., 50080, Zaragoza, Spain.
Stanley A. Barber	John B. Peterson Distinguished Professor Emeritus of Agronomy, Purdue University, West Lafayette, IN 47907.
J. M. Bennett	Professor, Department of Agronomy, University of Florida, Gainesville, FL 32611-0500.
Dale G. Blevins	Professor of Agronomy, Agronomy Department, University of Missouri, Columbia, MO 65211.
A. J. Bloom	Professor, Department of Vegetable Crops, University of California, Davis, CA 95616.
K. J. Boote	Professor of Agronomy, Agronomy Department, University of Florida, Gainesville, FL 32611.
R. Harold Brown	Professor, Department of Crop and Soil Sciences, University of Georgia, Athens, GA 30602-7272.
Martyn M. Caldwell	Professor of Ecology, Department of Range Science and The Ecology Center, Utah State University, Logan, UT 84322-5230.
Jeremy Colls	Senior Lecturer in Environmental Science, University of Nottingham, England.
Dennis B. Egli	Professor of Agronomy, Department of Agronomy, University of Kentucky, Lexington, KY 40546-0091.
L. T. Evans	CSIRO Division of Plant Industry, Canberra, Australia.
G. D. Farquhar	Professor, Australian National University, Canberra City, Australia.
Stephan D. Flint	Research Associate, Department of Range Science and The Ecology Center, Utah State University, Logan, UT 84322-5230.
Peter J. Gregory	Professor of Soil Science, Department of Soil Science, University of Reading, Whiteknights, P.O. Box 233, Reading, RG6 2DW, England.

Charles L. Guy	Associate Professor, Department of Environmental Horticulture, University of Florida, Gainesville, FL 32611-0512.
J. E. Harper	Supervisory Plant Physiologist, USDA-ARS, Plant Physiology and Genetics Research Unit, University of Illinois, Urbana, IL 61801.
Takeshi Horie	Professor of Crop Science, Laboratory of Crop Science, Faculty of Agriculture, Kyoto University, Kyoto, Japan.
R. J. Jones	Professor/Plant Physiologist, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108.
David B. Layzell	Professor of Biology, Biology Department, Queen's University, Kingston, Ontario, Canada K7L 3N6.
Paul H. Li	Professor of Horticultural Science and Plant Biological Science, Laboratory of Plant Hardiness, Department of Horticultural Science, University of Minnesota, St. Paul, MN 55108.
Jonathan Lynch	Assistant Professor of Plant Nutrition, Department of Horticulture, Pennsylvania State University, University Park, PA 16852.
Miller B. McDonald	Professor of Agronomy, Department of Agronomy, Ohio State University, Columbus, OH 43210-1086.
Angela H. M. Moloney	Plant Science Department, University of British Columbia, Vancouver, British Columbia, Canada V6T 2B1.
C. Jerry Nelson	Professor of Agronomy, Department of Agronomy, University of Missouri, Columbia, MO.
Henry T. Nguyen	Professor of Plant Genetics, Department of Plant and Soil Science, Texas Tech University, Lubbock, TX 79409.
J. B. Passioura	CSIRO Division of Plant Industry, Canberra, Australia.
Gary M. Paulsen	Professor of Agronomy, Department of Agronomy, Kansas State University, Manhattan, KS 66506.
John W. Radin	National Program Leader for Plant Physiology, USDA-ARS, National Program Staff, Beltsville, MD 20705.
Gina E. Sanders	Lecturer, Department of Life Sciences, Nottingham Trent University, England.
Thomas D. Sharkey	Professor, Department of Botany, University of Wisconsin, Madison, WI 53706.
Robert E. Sharp	Associate Professor of Plant Physiology, Department of Agronomy, University of Missouri, Columbia, MO 65211.
Thomas R. Sinclair	Plant Physiologist, USDA-ARS, and Professor of Agronomy, University of Florida, Gainesville, FL 32611-0840.
Stephen C. Spaeth	Plant Physiologist, Grain Legume Genetics and Physiology Research, USDA-ARS, Pullman, WA 99164-6434.
Judith F. Thomas	Professor of Botany and Director of Phytotron, North Carolina State University, Raleigh, NC 27695-7618.

M. Tollenaar Associate Professor, Department of Crop Science, University of Guelph, Guelph, Ontario, Canada.

Mike H. Unsworth Director, Center for Analysis of Environmental Change, Oregon State University, Corvallis, OR 97331-6511.

E. Van Volkenburgh Associate Professor of Botany, Botany Department, University of Washington, Seattle, WA 98195.

Mark E. Westgate Plant Physiologist, USDA-ARS, MWA, North Central Soil Conservation Research Laboratory, Morris, MN 56267.

E. T. York, Jr. Distinguished Service Professor, University of Florida, Gainesville, FL 32611.

Conversion Factors for SI and non-SI Units

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Unit	To convert Column 2 into Column 1, multiply by
		Length	
0.621	kilometer, km (10^3 m)	mile, mi	1.609
1.094	meter, m	yard, yd	0.914
3.28	meter, m	foot, ft	0.304
1.0	micrometer, μm (10^{-6} m)	micron, μ	1.0
3.94×10^{-2}	millimeter, mm (10^{-3} m)	inch, in	25.4
10	nanometer, nm (10^{-9} m)	Angstrom, Å	0.1
		Area	
2.47	hectare, ha	acre	0.405
247	square kilometer, km^2 $(10^3\ m)^2$	acre	4.05×10^{-3}
0.386	square kilometer, km^2 $(10^3\ m)^2$	square mile, mi^2	2.590
2.47×10^{-4}	square meter, m^2	acre	4.05×10^3
10.76	square meter, m^2	square foot, ft^2	9.29×10^{-2}
1.55×10^{-3}	square millimeter, mm^2 $(10^{-3}\ m)^2$	square inch, in^2	645
		Volume	
9.73×10^{-3}	cubic meter, m^3	acre-inch	102.8
35.3	cubic meter, m^3	cubic foot, ft^3	2.83×10^{-2}
6.10×10^4	cubic meter, m^3	cubic inch, in^3	1.64×10^{-5}
2.84×10^{-2}	liter, L (10^{-3} m^3)	bushel, bu	35.24
1.057	liter, L (10^{-3} m^3)	quart (liquid), qt	0.946
3.53×10^{-2}	liter, L (10^{-3} m^3)	cubic foot, ft^3	28.3
0.265	liter, L (10^{-3} m^3)	gallon	3.78
33.78	liter, L (10^{-3} m^3)	ounce (fluid), oz	2.96×10^{-2}
2.11	liter, L (10^{-3} m^3)	pint (fluid), pt	0.473

		Mass	
2.20×10^{-3}	gram, g (10^{-3} kg)	pound, lb	454
3.52×10^{-2}	gram, g (10^{-3} kg)	ounce (avdp), oz	28.4
2.205	kilogram, kg	pound, lb	0.454
0.01	kilogram, kg	quintal (metric), q	100
1.10×10^{-3}	kilogram, kg	ton (2000 lb), ton	907
1.102	megagram, Mg (tonne)	ton (U.S.), ton	0.907
1.102	tonne, t	ton (U.S.), ton	0.907
		Yield and Rate	
0.893	kilogram per hectare, kg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12
7.77×10^{-2}	kilogram per cubic meter, kg m^{-3}	pound per bushel, lb bu^{-1}	12.87
1.49×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 60 lb	67.19
1.59×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 56 lb	62.71
1.86×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 48 lb	53.75
0.107	liter per hectare, L ha^{-1}	gallon per acre	9.35
893	tonnes per hectare, t ha^{-1}	pound per acre, lb $acre^{-1}$	1.12×10^{-3}
893	megagram per hectare, Mg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12×10^{-3}
0.446	megagram per hectare, Mg ha^{-1}	ton (2000 lb) per acre, ton $acre^{-1}$	2.24
2.24	meter per second, m s^{-1}	mile per hour	0.447
		Specific Surface	
10	square meter per kilogram, m^2 kg^{-1}	square centimeter per gram, cm^2 g^{-1}	0.1
1000	square meter per kilogram, m^2 kg^{-1}	square millimeter per gram, mm^2 g^{-1}	0.001
		Pressure	
9.90	megapascal, MPa (10^6 Pa)	atmosphere	0.101
10	megapascal, MPa (10^6 Pa)	bar	0.1
1.00	megagram per cubic meter, Mg m^{-3}	gram per cubic centimeter, g cm^{-3}	1.00
2.09×10^{-2}	pascal, Pa	pound per square foot, lb ft^{-2}	47.9
1.45×10^{-4}	pascal, Pa	pound per square inch, lb in^{-2}	6.90×10^3

(continued on next page)

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Unit	To convert Column 2 into Column 1, multiply by
		Temperature	
1.00 (K − 273)	Kelvin, K	Celsius, °C	1.00 (°C + 273)
(9/5 °C) + 32	Celsius, °C	Fahrenheit, °F	5/9 (°F − 32)
		Energy, Work, Quantity of Heat	
9.52×10^{-4}	joule, J	British thermal unit, Btu	1.05×10^{3}
0.239	joule, J	calorie, cal	4.19
10^{7}	joule, J	erg	10^{-7}
0.735	joule, J	foot-pound	1.36
2.387×10^{-5}	joule per square meter, J m^{-2}	calorie per square centimeter (langley)	4.19×10^{4}
10^{5}	newton, N	dyne	10^{-5}
1.43×10^{-3}	watt per square meter, W m^{-2}	calorie per square centimeter minute (irradiance), cal cm^{-2} min^{-1}	698
		Transpiration and Photosynthesis	
3.60×10^{-2}	milligram per square meter second, mg m^{-2} s^{-1}	gram per square decimeter hour, g dm^{-2} h^{-1}	27.8
5.56×10^{-3}	milligram (H_2O) per square meter second, mg m^{-2} s^{-1}	micromole (H_2O) per square centimeter second, μmol cm^{-2} s^{-1}	180
10^{-4}	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square centimeter second, mg cm^{-2} s^{-1}	10^{4}
35.97	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square decimeter hour, mg dm^{-2} h^{-1}	2.78×10^{-2}
		Plane Angle	
57.3	radian, rad	degrees (angle), °	1.75×10^{-2}

Electrical Conductivity, Electricity, and Magnetism			
10	siemen per meter, $S\ m^{-1}$	millimho per centimeter, $mmho\ cm^{-1}$	0.1
10^4	tesla, T	gauss, G	10^{-4}
Water Measurement			
9.73×10^{-3}	cubic meter, m^3	acre-inches, acre-in	102.8
9.81×10^{-3}	cubic meter per hour, $m^3\ h^{-1}$	cubic feet per second, $ft^3\ s^{-1}$	101.9
4.40	cubic meter per hour, $m^3\ h^{-1}$	U.S. gallons per minute, $gal\ min^{-1}$	0.227
8.11	hectare-meters, ha-m	acre-feet, acre-ft	0.123
97.28	hectare-meters, ha-m	acre-inches, acre-in	1.03×10^{-2}
8.1×10^{-2}	hectare-centimeters, ha-cm	acre-feet, acre-ft	12.33
Concentrations			
1	centimole per kilogram, $cmol\ kg^{-1}$	milliequivalents per 100 grams, meq $100\ g^{-1}$	1
0.1	gram per kilogram, $g\ kg^{-1}$	percent, %	10
1	milligram per kilogram, $mg\ kg^{-1}$	parts per million, ppm	1
Radioactivity			
2.7×10^{-11}	becquerel, Bq	curie, Ci	3.7×10^{10}
2.7×10^{-2}	becquerel per kilogram, $Bq\ kg^{-1}$	picocurie per gram, $pCi\ g^{-1}$	37
100	gray, Gy (absorbed dose)	rad, rd	0.01
100	sievert, Sv (equivalent dose)	rem (roentgen equivalent man)	0.01
Plant Nutrient Conversion			
	Elemental	***Oxide***	
2.29	P	P_2O_5	0.437
1.20	K	K_2O	0.830
1.39	Ca	CaO	0.715
1.66	Mg	MgO	0.602