

# Horticultural Reviews VOLUME 40

### HORTICULTURAL REVIEWS Volume 40

Horticultural Reviews is sponsored by:

American Society of Horticultural Science International Society for Horticultural Science

# **Editorial Board, Volume 40**

Thomas M. Gradziel Kim E. Hummer Paolo Inglese

## HORTICULTURAL REVIEWS Volume 40

edited by Jules Janick Purdue University



Copyright © 2012 by Wiley-Blackwell. All rights reserved.

Published by John Wiley & Sons, Inc., Hoboken, New Jersey. Published simultaneously in Canada.

Wiley-Blackwell is an imprint of John Wiley & Sons, Inc., formed by the merger of Wiley's global Scientific, Technical, and Medical business with Blackwell Publishing.

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, scanning, or otherwise, except as permitted under Section 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the Publisher, or authorization through payment of the appropriate per-copy fee to the Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, (978) 750-8400, fax (978) 750-4470, or on the web at www.copyright.com. Requests to the Publisher for permission should be addressed to the Permissions Department, John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, (201) 748-6011, fax (201) 748-6008, or online at http://www.wiley.com/go/permission.

Limit of Liability/Disclaimer of Warranty: While the publisher and author have used their best efforts in preparing this book, they make no representations or warranties with respect to the accuracy or completeness of the contents of this book and specifically disclaim any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives or written sales materials. The advice and strategies contained herein may not be suitable for your situation. You should consult with a professional where appropriate. Neither the publisher nor author shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

For general information on our other products and services or for technical support, please contact our Customer Care Department within the United States at (800) 762-2974, outside the United States at (317) 572-3993 or fax (317) 572-4002.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic formats. For more information about Wiley products, visit our web site at www.wiley.com.

### Library of Congress Cataloging-in-Publication Data:

ISBN 978-1-118-34583-2 (cloth) ISSN 0163-7851

Printed in the United States of America

 $10 \quad 9 \quad 8 \quad 7 \quad 6 \quad 5 \quad 4 \quad 3 \quad 2 \quad 1$ 

### Contents

Co	Contributors			
	<b>Dedication: John Reuben Clark</b> Chad E. Finn			
1.		harvest Biology and Technology of Cut Flowers Potted Plants	1	
		aael S. Reid and Cai-Zhong Jiang	T	
		Introduction	3	
		The Ornamental Industry	4	
		Factors Affecting the Postharvest Life of Ornamentals	5	
		Biology of Flower Senescence	29	
		Transgenic Strategies for Extending Floral Life	36	
	VI.	Future Prospects	42	
	Liter	ature Cited	44	
2.	Wat	er Relations of Cut Flowers: An Update	55	
	Wou	ter G. van Doorn		
	I.	Introduction	57	
		Water Supply to Flowers	57	
		Water Loss: Influence of Stomata	58	
		Water Uptake: Xylem Blockage	63	
	V.	Small and Coalescing Air Bubbles Form in Cut		
		Stems, in the Absence of Cavitation	88	
	VI.	Water Flow Rate in the Xylem as Affected by		
		Ions in the Water	89	
	VII.	Use of An Artificial Tap Water as a Standard		
		Vase Solution?	90	
		Water Stress and Ethylene	93	
	IX.	Conclusions	96	

	Acknowledgments	97
	Literature Cited	97
3.	<b>Factors Involved in Fruit Calcium Deficiency Disorders</b> Sergio Tonetto de Freitas and Elizabeth J. Mitcham	107
	I. Introduction	109
	II. Physiology of Calcium Deficiency in Fruit Tissue	100
	III. Calcium Translocation at the Whole Plant Level	111
	IV. Calcium at the Fruit Level	116
	V. Calcium at the Cellular Level	118
	VI. Role of Abiotic Stress in Calcium Deficiency Disorders	125
	VII. Role of Growth Regulators in Calcium Deficiency	
	Disorders	127
	VIII. Proposed Mechanisms Controlling Fruit Susceptibility	
	to Calcium Deficiency Disorders	135
	Literature Cited	137
4.	Rhubarb: Botany, Horticulture, and Genetic Resources	147
	Danny L. Barney and Kim E. Hummer	
	I. Introduction	148
	II. Historical	149
	III. Botany	156
	IV. Horticulture	164
	V. World Genetic Resources	170
	VI. The Future	178
	Acknowledgments	178
	Literature Cited	179
	Manuscripts	182
5.	Ancient Dates and their Potential Use in Breeding	183
	Shimshon Ben-Yehoshua and Liat Josefsberg Ben-Yehoshua	
	I. Introduction	184
	II. Dates and Health	189
	III. Historical Review	190
	IV. Remnants of Dates and Their Potential Uses	203
	V. Conclusions	210
	Acknowledgments	210
	Literature Cited	210

6.	The Cucurbits and Nightshades of Renaissance England:			
	John Gerard and William Shakespeare	215		
	Jules Janick, Harry S. Paris, and Marie-Christine Daunay			
	I. Introduction	216		
	II. John Gerard	217		
	III. William Shakespeare	246		
	IV. The Connection Between Gerard and Shakespeare	251		
	V. Conclusion	252		
	Literature Cited	255		
7.	Greenhouse Cover Technology	259		
	Johannes F. J. Max, Ulrich Schurr, Hans-Jürgen Tantau,			
	Urbanus N. Mutwiwa, Thomas Hofmann, and Andreas Ulbrich			
	I. Introduction	263		
	II. Greenhouse Superstructures	267		
	III. Materials Used for Covering Greenhouses	286		
	IV. Material Combinations	346		
	V. Plant Response to Greenhouse Covers	350		
	VI. Comparison and Economic Assessment	368		
	VII. Conclusions and Prospects	378		
	Acknowledgments	381		
	Literature Cited	381		
Subject Index				
Cu	imulative Subject Index	399		
Cu	imulative Contributor Index	427		

### Contributors

- Danny L. Barney, USDA-ARS Arctic and Subarctic Plant Gene Bank, 1509 South Trunk Road, Palmer, Alaska, 99645, USA
- Liat Josefsberg Ben-Yehoshua, The Davidson Institute of Science Education at the Weizmann Institute of Science (R.A.), P.O.B. 26, Rehovot 76100, Israel
- Shimshon Ben-Yehoshua, Emeritus, Department of Postharvest Science, Volcani Center, Agricultural Research Organization, Bet Dagan 50250, Israel
- Marie-Christine Daunay, INRA, UR 1052 Unité de Génétique et d'Amélioration des Fruits et Légumes, F-84140 Montfavet, France
- **Thomas Hofmann**, Centrosolar Glas GmbH & Co KG, Siemensstr. 3, 90766 Fürth, Germany
- Kim E. Hummer, USDA-ARS National Clonal Germplasm Repository, 33447 Peoria Road, Corvallis, Oregon 97333, USA
- Jules Janick, Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, Indiana 47907, USA
- Cai-Zhong Jiang, Crops Pathology and Genetic Research Unit, USDA-ARS, Davis, California 95616, USA
- Johannes F. J. Max, Institut für Bio- und Geowissenschaften, IBG-2: Pflanzenwissenschaften, Forschungszentrum Jülich GmbH, 52425 Jülich, Germany
- **Elizabeth J. Mitcham**, Department of Plant Sciences, University of California, One Shields Avenue, Davis, California 95616, USA
- **Urbanus N. Mutwiwa**, Biomechanical and Environmental Engineering Department Jomo Kenyatta University of Agriculture and Technology, P.O. Box 62,000, Nairobi, Kenya
- Harry S. Paris, Department of Vegetable Crops and Plant Genetics, Agricultural Research Organization, Newe Ya'ar Research Center, PO Box 1021, Ramat Yishay 30095, Israel
- Michael S. Reid, Department of Plant Sciences, University of California, Davis, California 95616, USA
- **Ulrich Schurr**, Institut für Bio- und Geowissenschaften, IBG-2: Pflanzenwissenschaften, Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

- Hans-Jürgen Tantau, Biosystems and Horticultural Engineering Section, Leibniz University Hannover, Herrenhäuser Str. 2, D-30419, Hannover, Germany
- Sergio Tonetto de Freitas, Department of Plant Sciences, University of California, One Shields Avenue, Davis, California 95616, USA
- Andreas Ulbrich, Fachhochschule Osnabrück, FL Agrarwissenschaften, FG Gemüseproduktion und-Verarbeitung, Oldenburger Landstraße 24, 49090 Osnabrück, Germany
- Wouter G. van Doorn, Mann Laboratory, Department of Plant Sciences, University of California, Davis, California 95616, USA



John Reuben Clark

### Dedication: John Reuben Clark

This volume is dedicated to John Reuben Clark for his outstanding contributions to horticulture. While known particularly for his impact on blackberry, blueberry, table grape, and peach cultivar development, he has also been a strong and enthusiastic voice for horticulture through the American Society for Horticultural Science (ASHS) and has had remarkable insight into the development of intellectual property rights for fruit crops.

John Reuben Clark is a "highly interesting organism." Born in Jackson, Mississippi into a dairy farming family from nearby Madison to William Theodore "Willy T" and Ethel Wallace Clark on April 13, 1957, this southern, rural dairy heritage has been part of who John was and has become. "I grew up on a dairy farm in Mississippi, and milking cows along with growing corn, cotton, soybeans, and cutting hay provided more than enough inspiration to become something, or anything, besides a farmer associated with these crops. Our domestic quadrupeds of the bovine type that provided a twice-daily product-extraction opportunity contributed to a particularly strong inspiration to head in another direction. As best I can remember, it looked like going to college was the logical path to take." (ASHS Newsletter Reflections, August 2008). These words hint at the stories John can spin and how he can use metaphors for many human activities. John has very unique ways of describing people or things all of which usually bring smiles to people's faces (although these are occasionally preceded by a dumbfounded look on the receiving end as they process what John has said!).

As is true of many dairy family kids, his main extracurricular activity during his school years was heading home to milk cows. He graduated from high school in Madison in 1975 and, after a year at junior college, headed north to Mississippi State University. John earned his B.S. in Horticulture in 1978 and followed that by earning his M.S. in 1980 with a project entitled: "The changes in berry characteristics during maturation of cultivars of muscadine grape (*Vitis rotundifolia* Michx)". At Mississippi State, his advisor, Dr. Patrick Hegwood, was very influential in nurturing John's career and was later responsible for introducing him to Dr. James N. Moore at the University of Arkansas. Dr. Jean Overcash, the long-time fruit researcher and teacher, was also inspiring. During his time at Mississippi State, John started two lifelong love affairs. The first one was a lifelong love of muscadine grapes that he has been able to return to much later in his career. Second, and more important, Mississippi State was where he met the lovely Sharon Hodnett, from Starkville, MS, whom he married in the campus Chapel of Memories in 1978.

The young couple left Mississippi State and headed further north to the University of Arkansas, where John began his studies and served as a research technician under the guidance of Jim Moore who ran one of the most remarkable berry and tree fruit breeding programs in the country. Under his guidance, John finished his dissertation on "Inheritance of resistance in highbush blueberry to Phytophthora cinnamomi" and graduated in 1983. While in graduate school, Sharon and John's son Johnathan was born. After graduation, John was quickly hired as the Resident Director of the University of Arkansas Fruit Substation in Clarksville, beginning the first stage of his career. In his role as Resident Director, John gained valuable experience managing people and working closely with the crops he would later focus on in his breeding efforts. A few years into this position, his appointment was changed as he took on the role of an Associate Professor as well as Director of the Substation. He was then also expected to continue his successful research program along with managing the station. The skills he learned to deal with folks working on the station and scientists on campus who had research projects there were invaluable as he had to manage a bigger and more complex program and activities on campus and worldwide later in his career. John's early research program had a few strong emphases including grape, blueberry, and blackberry nutrition, the impact of nematodes and mulch on blueberry health, and seed morphology and development in blackberry. He also began his long collaboration with Dr. Moore, developing berry and peach/nectarine cultivars. His blueberry and blackberry nutrition work was critical to the developing industries in the lower Midwest as it took into account the old, eroded, Ozark soils and monitored the foliar and soil nutrient content throughout the year. The combination of these

allowed growers to make better nutrition management decisions based on tissue-nutrient analysis.

In 1994, John gave up his estate on the Fruit Substation for city living when he and his family moved to campus in Fayetteville. While John no longer had the day-to-day responsibilities for running the Substation he did take on teaching Small Fruit Production and Advanced Plant Breeding and had the opportunity to mentor graduate and undergraduate students. While John's students have been a joy to him, he has been known to comment "New students can be like the mammary glands of a quadruped. They can require near constant attention." Three years later, Dr. Moore retired and John took on full responsibilities for the breeding programs. On the firm foundation of Moore's germplasm, John and his collaboration expanded the program, now considered among the world's most highly regarded.

#### I. BREEDING PROGRAMS

The University of Arkansas blackberry breeding program is responsible for developing a cultivated crop where there was none before. Dr. Moore assembled the germplasm and developed the first decent quality erect blackberry cultivars in the 1970s. In the 1980s, in addition to greatly improving fruit quality, the thornless trait was incorporated into cultivars by Jim and John. 'Navaho', which they released in 1989, has been one of the most important cultivars ever. While starting to fall from favor, it is still known for its very high quality and reliable yield. John's more recent releases, 'Natchez' and 'Ouachita', have been widely planted in the eastern United States, California, and around the world in suitable climates. In the early 1990s, the University of Arkansas found and characterized the primocane fruiting characteristic in blackberry. While not an unheard of trait, strong expression for the trait in blackberries that yielded well and had good quality fruit was unheard of. In 2004, John released the first two primocane-fruiting blackberry cultivars 'Prime-Jan<sup>®</sup>' and 'Prime Jim<sup>®</sup>'. While these were very interesting, their fruit quality did not meet standards for commercial production. The 2009 release, 'Prime-Ark 45®', had commercial fruit quality. While the future of primocane fruiting cultivars in the commercial blackberry industry is unclear, this trait developed in red raspberry led to a worldwide revolution in production for the fresh market. We hope these primocane fruiting cultivars are just the first part of a similar revolution in blackberries. Overall, John has released 16 blackberry cultivars that have had commercial impact.

Peaches and nectarines, grown in a good climate, harvested from the tree, and "chin dripping" ripe are a remarkable thing. Unfortunately, some might say too much effort has gone into developing peaches and nectarines that ship and look good without regard to eating quality, leading to a decline in the consumption of these crops nationally. While the University of Arkansas initially focused on developing clingstone peaches for the baby food industry, John's program is focused on trying to bring that great peach-eating experience back to consumers. John has released seven peach and four nectarine cultivars, including three white, freestone peaches. He has incorporated the nonmelting flesh trait into several of these cultivars for those interested in a peach that may ship better with good eating quality. He has also worked to incorporate resistance to bacterial leaf spot, a serious disease in warm, humid climates.

For many years, the primary goal of the Arkansas table grapebreeding program was to develop cultivars that were seedless, tasted good, and were adapted to the hot, humid lower Midwest summers. Despite John's belief that "breeding grapes is the devil!" and that "grapes can produce some sho-nuff funky flavors," the program has been tremendously successful; the Arkansas cultivars are now the standard for much of the Midwest and for much of the rest of the United States as the basis for grapes grown with reduced fungicide programs and increased hardiness over pure Vitis vinifera cultivars. While they have done well, growers in the Midwest have a hard time competing with growers in California. This reality might have caused John to close up shop; instead he took his unique shapes, sizes, colors and flavors to California where he has worked with breeders there to develop new and novel grapes. Selections based on his elongated fruit types will be finding their way to consumer's shelves in the near future. Under John's watch, seven grape cultivars have been released from the University and a great deal of fantastic germplasm is now being worked into selections that have great potential in the grapegrowing regions of the world.

While John's primary emphasis has been on blackberries, table grapes, and peaches/nectarines, he has also worked on other crops. He and Dr. Moore released 'Ozarkblue', which has become a major cultivar worldwide for late-mid-season production, and A-257 (Kabluey<sup>TM</sup>) blueberries. He has also collaborated on the release of 'Ovation' strawberry, 'Summit' blueberry, 'Triple Crown' blackberry, and 'Pacific Deluxe', 'Pacific Royale,' and 'Pacific Majesty red raspberries. With Sharon's endorsement, John has also recently been able to rekindle an old flame first ignited in grad school when he increased his

program's emphasis on breeding muscadine grapes. While there are no cultivars yet released, even a northerner has to admit that some of his selections are starting to taste okay.

While there are many insights you can get from John about what makes a good breeder, one he often emphasizes with students is that you need the ability to stay outside in toughest of conditions day after day and still keep your focus on the plants in front of you. While somewhat simplistic, it really is true that breeders need to be able to physically and mentally spend huge amounts of their lives in the field regardless of the weather. In the current age of genotyping with molecular methods becoming an expanding and invaluable component of plant breeding, John believes that the art of "phenotyping" as a basic tool is much like playing an instrument and is best practiced with recurring opportunity.

### **II. INTELLECTUAL PROPERTY**

Back in the early 1980s when agricultural experiment station funding begin to be tightened at the University of Arkansas, extramural support for the fruit-breeding program surfaced as an issue. Dr. Moore received a note from a major U.S. nursery thanking them for helping them make lots of money off of an Arkansas cultivar. Since program funding was a concern, Dr. Moore sent out notes to nurseries and growers trying to drum up financial support for the program. Almost no one responded except for a small farm grower who sent Jim a check for \$50. This got Jim to thinking and he began to patent the University of Arkansas cultivars. This served the program well as they began to get some cash flow from the royalties on these cultivars. John continued this practice. However, in the late 1990s and early 2000s, the importance of grantsmanship rose in academia. Grants were now not only a measure of the success of a program, but they were also the financial lifeblood of many programs. Unfortunately, receiving grants to consistently fund a breeding program is not a reliable thing, particularly in a state with no organized fruit industry to provide grant support for the breeding efforts. John took this all in, looked around at his colleagues scrambling after grants, and thought there had to be a better way. With this in mind he worked very intensively with the intellectual property rights office at the University of Arkansas and began to find ways to maximize the return the breeding program could realize from germplasm, selections, and cultivars. All sorts of relationships and models were developed and put in

place regionally, nationally, and internationally, and with private and public partners. Nearly \$2,000,000 dollars in royalties have been generated in the past 14 years and nearly another \$1,000,000 in the past 10 years in breeding and testing agreements with private companies. While this kind of funding is not enough to totally run a program such as John's at the University of Arkansas, it does make the difference between having and not having a breeding program. More appealing and perhaps as important, income generated from royalties has kept John from having to chase grant dollars quite as vigorously as some colleagues. While the financial bottom line is all that matters to some, for others, especially those in academia, "scholarly activity" is equally important. John has worked hard in his presentations and writings to effectively make the case that cultivar releases and the subsequent royalties are as much a scholarly activity as are refereed publications and successful grant applications.

### **III. HORTICULTURE AT LARGE**

Service to one's professional community is something John has taken very seriously. Starting at home in the Department of Horticulture at the University of Arkansas he has served in many capacities including a year as the interim Department Head. He has given many extension presentations despite having no extension appointment. Well known for spreading the goodness of the University of Arkansas worldwide, he has taught folks how to call the Hogs with the famous Razorback 'Pig Sooie' Cheer many times complete with body motions and strange sounds. His activities within the university, throughout his professional organizations, and internationally led him to be nominated and elected as a University Professor (this is not the same as reaching professor rank, only a few professors on campus carry this honor) at the University of Arkansas. This puts him in very exclusive class of folks in academia.

The ASHS has benefited greatly from John's passion. He served on every appropriate working group as chair and worked very hard within the Southern Region of ASHS serving on many of their committees and eventually was President in 2003. He used this experience as a springboard to the national ASHS Board of Directors, elected first as Research Division Vice President and then being elected to serve as President of ASHS in 2008–2009. A key area of focus while serving on the ASHS Board was in developing a national issues program to help monitor and influence issues in the enhancement of specialty crops both in federal policy and funding. His ASHS Reflections columns published in the ASHS newsletter while he was President are a fun and interesting read. That man sure is exuberant, can keep you interested, and knows when to stop writing before you are bored . . . a lot like a good minister or motivational speaker. The following aphorisms from John speak strongly as to why folks flock to him and want to work with him: "I am a big believer in trying to focus on recognizing the positive in situations and happenings. The basis being that positive feelings bring forth positive results both now and later." (ASHS Newsletter Reflections, September 2008) and "It seems that we are inundated with bad news about all sorts of things on a continual basis. I am always amazed at how little is said of 'good happenings'! But I do know this: looking for the good, expecting to see it in something around the corner, having faith that what one seeks will be found, are fundamental foundations for my thinking and living (and when I veer from this focus I try to work my way back to this as soon as I can)." (ASHS Newsletter Reflections, December 2008).

Anyone reading so far will hopefully have gotten the feeling that John is a tremendously positive, productive, entertaining, warm, and kind man who draws folks to him like moths to a flame. The good will he has engendered opens doors around the world where he and Sharon are welcomed on their beloved traveling adventures. They carry over throughout his interactions with colleagues where he is seen as someone who you want to collaborate with not only because he is good and does what he says he is going to do but because he is flat out fun to work with. They also carry over to the golf course where he can "bat the little white orb" around with the best of them. He is welcoming and one would be amazed at the number of international and domestic travelers who found their way out to the Clarksville Substation in some miserable weather just to have fun in the briar patch, peach orchard, or muscadine vineyard with John. While I am sure John's mother taught him well, I think Sharon has done a great deal to teach John the graciousness with which he carries himself around folks. John is a plant breeder through and through and nothing gives him more pleasure than spending time in the field in his plots and seeing cultivars of his bring some profit to growers and some joy to consumers.

Finally, it would seem unfair to not share with an even greater audience some of John Reuben Clark's wisdom and witticisms. Friends and colleagues including: E. Acevedo, F. Cooper, M.K. Ehlenfeldt, C.E. Finn, E.J. Hanson, R. Hargreaves, K.S. Lewers, J.J. Luby, D.S. NeSmith, G. C. Pavlis, M.P. Pritts, S. Sleezer, E.T. Stafne, B. Strik, and E. Thompson are responsible for all unattributed quotes. On administration:

"I have seen the book on that. It's one page long and blank on both sides."

On missed opportunities:

"That cow has done left the barn"

On finding the best opportunities:

"I've got a bunch of fish in this barrel and I'm lookin' for the biggest."

"If I have enough poles in the water I am bound to catch something!"

On a project or person that just is not working:

"That dog won't hunt."

Philosophical:

"I believe in divine intervention and backing into stuff."

"Back my truck up to a loading dock and get loaded up on good."

On good things happening to friends:

"They're a much better metaphysical attractor than I am."

Bovine comments:

- When he says: "Is the cow in the barn?" what he really means is: "Is there coffee creamer in the fridge?
- If a program generally has to scrounge for money to work with he refers to it as "*having mange*." He assures his friends and colleagues that "*our program does not have mange*."

On facing problems:

"One day I was standin' there in the middle of a briar patch . . . "

On losing a research project to hail:

"Everything was fine until the propeller hit a stump."

While trying to pick up a friend who was down:

"May you slide into a pile of happiness this holiday season."

On retiring:

"When ya thinkin' ya might reel in the hose?"

On the challenges of getting reviewers to do their job:

"I finally got your manuscript out of the eddy today. Gave up on those peckerwoods that look like they got their line tangled in an old willow tree, and used some local bait to hook the final review."

On saying "no" when you're busy:

"Some folks have just got to realize your dance card's full"

On *Rubus* in North America having been all mixed up genetically with interspecific crosses:

"Like a big 'ol Rubus sex party"

CHAD E. FINN

U. S. Department of Agriculture Agricultural Research Service Horticultural Crops Research Laboratory Corvallis, Oregon, 97330, USA

### **Postharvest Biology and Technology** of Cut Flowers and Potted Plants

Michael S. Reid Department of Plant Sciences University of California Davis, California 95616, USA

*Cai-Zhong Jiang* Crops Pathology and Genetic Research Unit USDA-ARS Davis, California 95616, USA

### ABSTRACT

The relatively brief postharvest life of most cut flowers and potted flowering plants can be extended by a range of technologies. Studies have shown that vase life is negatively correlated with respiration after harvest, so prompt cooling to the lowest safe storage temperature is a key to long-distance transport of these perishable crops. Forced air cooling is the method of choice for cut flowers, and vacuum cooling has been shown to be very effective for cooling potted plants. In contrast to some other horticultural crops, controlled and modified atmospheres seem to have little effect on petal respiration, and these techniques have not proved commercially useful in the marketing of many cut flowers. Low temperatures are also important in managing the effect of other factors contributing to early senescence, including water loss, the effects of ethylene, leaf yellowing, and the growth of diseases, particularly caused by Botrytis cinerea. Ornamentals originating in the tropics and subtropics cannot be cooled below 10°C because they rapidly show the symptoms of chilling injury. Chemical strategies to improve the life of ornamentals include the application of abscisic acid to reduce water loss, particularly in potted and bedding plants, pretreatment with the volatile ethylene inhibitor 1-methylcyclopropene (1-MCP) to prevent the

Horticultural Reviews, Volume 40, First Edition. Edited by Jules Janick.

<sup>© 2012</sup> Wiley-Blackwell. Published 2012 by John Wiley & Sons, Inc.

effects of endogenous or exogenous ethylene, treatment with gibberellins or cytokinins (CKs), which often delay leaf yellowing and may increase bud opening and flower life. Thidiazuron, a nonmetabolized CK, has proven particularly effective for this purpose. A new strategy for inhibiting the growth of B. cinerea on floral tissues is to treat them with low concentrations of hypochlorite. Floral senescence is an active process with many of the hallmarks of programmed cell death. Molecular analysis has revealed a large number of candidate genes with possible roles in senescence and remobilization. Virusinduced gene silencing has been used to evaluate the potential role of some of these genes, particularly regulatory genes such as transcription factors and kinases, although none has yet been identified as a key controller. Ornamentals are particularly suited to testing transgenic strategies for extending shelf-life, and we report results of experiments using constructs where inducible promoters are used to drive genes that extend flower life. Of particular interest is the dramatic extension of longevity resulting from silencing a component of the 26S proteasome, which indicates the importance of targeted protein degradation in control of floral senescence, and could serve as a strategy for extending the life of ethylene-insensitive ephemeral flowers. Future research will undoubtedly focus on providing better germplasm by using traditional, genomic assisted, and/or molecular breeding approaches for improving the postharvest performance of ornamentals.

**KEYWORDS:** biotechnology; gene regulation; growth regulators; temperature; water relations

#### ABBREVIATIONS

- I. INTRODUCTION
- II. THE ORNAMENTAL INDUSTRY
- III. FACTORS AFFECTING THE POSTHARVEST LIFE OF ORNAMENTALS
  - A. Genotype
  - **B.** Preharvest Factors
  - C. Temperature
  - D. Controlled and Modified Atmospheres
  - E. Chilling Injury
  - F. Water Relations
    - 1. Cut Flowers
    - 2. Potted Plants
  - G. Ethylene and Other Hormones
    - 1. Ethylene
    - 2. Abscisic Acid
    - 3. Cytokinins
    - 4. Other Hormones and Regulators
  - H. Disease
  - I. Growth and Tropic Responses
  - J. Carbohydrate Supply

#### 1. POSTHARVEST OF CUT FLOWERS AND POTTED PLANTS

#### IV. BIOLOGY OF FLOWER SENESCENCE

- A. Ultrastructural Changes
- B. Changes in the Transcriptome
  - 1. Gene Expression Analysis
  - 2. Functional Analysis
- C. Changes in the Proteome
- D. Senescence Regulation
- V. TRANSGENIC STRATEGIES FOR EXTENDING FLORAL LIFE
  - A. Extending the Life of Ethylene-Sensitive Flowers
  - B. Extending the Life of Ethylene-Insensitive Flowers
  - C. Other Transgenic Targets
- VI. FUTURE PROSPECTS

LITERATURE CITED

### ABBREVIATIONS

### I. INTRODUCTION

Much has changed in our understanding of the postharvest biology of floral and foliage crops since the publication, in the first and third volumes of *Horticultural Reviews*, of the two parts of Halevy and Mayak's comprehensive review of this topic (Halevy and Mayak 1979, 1981). Since then other reviews on aspects of the basic biology of flower senescence (Borochov and Woodson 1989; van Doorn and Stead 1994; van Doorn and Woltering 2004), and on the role of ethylene (Reid and Wu 1992) have been complemented by practical handbooks on postharvest technology for flowers (Nell and Reid 2000). In addition to articles in the peer-reviewed literature, the proceedings of the quadrennial meeting of postharvest floriculture members of ISHS, published in *Acta Horticulturae*, volumes 181 (1986), 261 (1989), 298 (1991), 405 (1995), 543 (2001), 669 (2005), and 847 (2009), provide concentrated sources of information on new developments in the field, and descriptions of the postharvest behavior of a wide range of floricultural crops.

Our goal in the present review is to describe studies that have changed our understanding of the postharvest biology of floricultural crops or added to the palette of postharvest technologies since previous reviews, and to indicate current optimal technologies based on that new understanding. In particular, we have focused on recent findings in relevant areas of basic plant biology, and conclude with a discussion of the way in which molecular strategies are being, or could be deployed in the future, to extend postharvest life and reduce postharvest losses of perishable ornamental crops.

### **II. THE ORNAMENTAL INDUSTRY**

In the past 50 years, the cut flower market has changed dramatically, from a local market with growers located on city outskirts, to a global one; flowers and cut foliage sourced from throughout the world are sold as bunches or combined into arrangements and bouquets in the major target markets, such as North America, Japan, and the European Union. Items in a single florist arrangement are often sourced from countries in three or more continents. The high value of cut flowers has driven major increases in production in many developing countries. Production of cut flowers and foliage can be highly profitable in countries with an ideal growing environment (particularly those close to the equator where the environment is uniform throughout the year), and labor costs are low. The costs of establishing production in the field or even in plastic houses are relatively modest, and harvest may start within a few months of planting.

This reshaping of the market has occurred with little consideration for its postharvest consequences. Flowers that used to be obtained from local growers and were retailed within days of harvest may now take as long as three weeks to arrive at the retail florist or supermarket. Increased emphasis on holidays as occasions for sale of cut flowers has exacerbated this trend. The volume of flowers required to meet the demand for the major holidays (Valentine's day, Mothers' day) has led to widespread storage. The peak in harvest of roses for Valentine's day in Central America, is three weeks prior to the holiday itself!

Because of their perishability, flowers and foliage produced in distant growing areas have traditionally been shipped by air (a transportation system whose rapidity fails to offset the disadvantages of poor temperature management and low humidities). The increasing cost of jet fuel, and the volumes of flowers being produced in countries such as Colombia and Kenya has led to many efforts to ship ornamentals in marine containers, further extending the time from harvest to market. These market and transportation changes have not been accompanied by changes in postharvest technologies to offset the time/temperature effect on the life of ornamentals. The net result, especially in North America, has been a reduction in display life of cut flowers and foliage, disenchantment with the cut flower purchase experience, documented in many surveys, and a per capita consumption of cut flowers in the United States that is less than that in almost all other developed countries (Reid and Jiang 2005).

### III. FACTORS AFFECTING THE POSTHARVEST LIFE OF ORNAMENTALS

The intersection of art, design, and horticulture represented by the ornamental plant industry has led to the use of a very wide variety of plant organs and taxa for ornamental purposes. Plants used range from the *Lycopsida* to the flowering plants, genera from *Acanthus* to *Zingiber*, and tissue types from young buds to fruits and seeds. This diversity of taxa, physiological state, and organ means that generalizations about their biology and even technology are often misleading. In this review, we focus largely on cut and potted flowers and foliage. The unique characteristics of the more unusual ornamental plant materials, and other horticultural crops properly classified as ornamentals (bulbs, corms, tubers, bedding plants, bare-root and dormant nursery materials, and the like) and their unique physiology and technology requirements will be mentioned only where recent research has provided information of interest and importance to their postharvest handling.

Some ornamentals, particularly potted and cut foliage can be extraordinarily long-lived. The *Aspidistra* of Victorian parlors have been replaced in our time by immortal *Scindapsis* (*Pothos*) plants that trail through offices and hotel lobbies everywhere. Nevertheless, the majority of the ornamentals of commerce have relatively short lives. The delicate petals of flowers are easily damaged, and are often highly susceptible to disease. Even under optimum conditions, their biology leads to early wilting, abscission, or both. Foliage is longer lived, although the low light of the postharvest environment frequently leads to early leaf yellowing, and, in some cases, leaf abscission. As with other perishable horticultural crops, the life of ornamentals is affected by physical, environmental, and biological factors. Choice of plant material, and preharvest factors play an important role. After harvest, temperature is of over-riding importance, and affects plant water relations, growth of disease, response to physical stresses, carbohydrate status, and the interplay among endogenous and exogenous growth regulators. Much has been learnt in the past 30 years about the role of these factors and the response of ornamentals to them, and some of the research findings have led to technologies that can greatly improve marketing and postharvest quality of ornamentals.

### A. Genotype

It is common knowledge that the postharvest life of flowers varies enormously, from the ephemeral flowers of the daylily to the extremely long-lived flowers of some orchid genera. Less extreme, but still marked variations are also seen within genera and even species, and certainly this variation provides a great opportunity for breeders to develop longer lasting flowers. Color, form, productivity, and disease resistance continue to be the targets of breeding programs. This can be seen by comparing the postharvest life of different cultivars from the same breeder. In Alstroemeria, we showed that time of petal fall and time of leaf vellowing both showed variation of more than 100% in lines released by the same breeder. Elibox and Umaharan (2008) reported vase lives of anthurium cultivars ranging from 14 to 49 days. A simple model, based on abaxial stomatal density and flower color accurately predicted the relative vase life ranking of different cultivars, providing an excellent tool for future breeding. Variations in other important postharvest characteristics have also been reported, for example, for ethylene sensitivity in carnations (Woltering and van Doorn 1988; Wu et al. 1991; Reid and Wu 1992) and in roses (Evans and Reid 1988; Macnish et al. 2010c). In their study, Macnish et al. (2010c) demonstrated a difference in vase life of modern rose cultivars of from 5 to 19 days. Five of the 38 cultivars tested were insensitive to ethylene indicating the breeding opportunities not only for extending vase life, but also eliminating the problem of ethylene-induced senescence and abscission. Mokhtari and Reid (1995) analyzed the difference in