



# Polyploidy and Hybridization for Crop Improvement

Annaliese S. Mason (Ed.)



# Polyploidy and Hybridization for Crop Improvement

Editor
Annaliese S. Mason
Department of Plant Breeding
Justus Liebig University Giessen
Giessen, Germany



CRC Press Taylor & Francis Group 6000 Broken Sound Parkway NW, Suite 300 Boca Raton, FL 33487-2742

© 2016 by Taylor & Francis Group, LLC CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works

Printed on acid-free paper Version Date: 20160225

International Standard Book Number-13: 978-1-4987-4066-1 (Hardback)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access www.copyright.com (http://www.copyright.com/) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

**Trademark Notice:** Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

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

Names: Mason, Annaliese, editor.

Title: Polyploidy and hybridizaton for crop improvement / editor: Annaliese Mason.

Description: Boca Raton, FL: CRC Press, Taylor & Francis Group, [2016] | Includes bibliographical references and index.

Identifiers: LCCN 2016007064 | ISBN 9781498740661 (hardcover)

Subjects: LCSH: Crop improvement. | Polyploidy. | Plant hybridization.

Classification: LCC \$B106.147 P59 2016 | DDC 631.5/23--dc23

LC record available at http://lccn.loc.gov/2016007064

Visit the Taylor & Francis Web site at http://www.taylorandfrancis.com

and the CRC Press Web site at http://www.crcpress.com

# Polyploidy and Hybridization for Crop Improvement

### **Preface**

Polyploidy and interspecific hybridization are critical processes in plant evolution and speciation. Polyploidy refers to the presence of more than two sets of chromosomes or the presence of more than one genome within a single organism, and interspecific hybridization refers to the process by which two different species come together to form a new organism with genetic information from both parents. When two different species each contribute a complete set of chromosomes to make a new, stable species with all the genetic information from both parents, this is referred to as "allopolyploid" formation, while "autopolyploids" have three or more sets of chromosomes from the same species. However, categorization of individuals or species as "auto" vs "allo" polyploid or as "intra" or "inter" specific hybrids is on some level arbitrary, depending on species definitions and genetic divergence between the parent genomes. In the middle are hybrids between subspecies or genetically distinct populations of individuals, or between geographically isolated taxonomic species with conserved genome structure.

Many of our current agricultural crops are either natural or agricultural hybrids or polyploids, including potato, oats, cotton, oilseed rape, wheat (and triticale), strawberries, kiwifruit, banana and many others. There is also a great deal of potential to utilise these natural evolutionary processes for targeted crop improvement, for example through introgression of desired traits from wild species into crops, production of seedless fruits, or even creation of entirely new crop types.

Polyploidy and interspecific hybridization are increasingly being revealed as both complex and common phenomena in plants. Characterization of crop genomes with modern genetics and genomics technologies has revealed that polyploidy and interspecific hybridization processes shaped many of our extant crop species. In parallel, breeding approaches utilizing polyploidy and interspecific hybridization as tools for crop improvement are becoming more and more common. Some crop genera have hundreds of years of manipulation of interspecific hybridization and polyploidy processes behind

#### vi Preface

them, while in others use of these processes for crop improvement is still at the theoretical stage. As our knowledge grows and technology advances, it is increasingly important to bring together expert researchers and plant breeders to form a cohesive picture of how best to utilize these evolutionary processes for crop improvement across diverse genera. Which processes and problems are crop-specific, and which are widely applicable? Answering these questions has potential to not only aid in our understanding of plant evolutionary processes, but to add additional fundamental tools to the plant breeding tool kit, helping the agricultural processes on which we all rely for life. This book will provide a comprehensive summary of how the processes of polyploidy and hybridisation have shaped the foods we eat, and how these processes have been and can be used for crop improvement. This book is targeted to both researchers and breeders, facilitating sharing of knowledge and stories across the wide range of crops where polyploidy and hybridization processes are relevant and potentially useful for crop improvement.

# **Contents**

Pref	face	V
1.	Interspecific Hybridization for Upland Cotton Improvement	1
	Abstract	1
	The Cotton Crop	2 3 5
	Origin and Taxonomy of Gossypium hirsutum	3
	Domestication and "Upland" Cotton	5
	Cotton Improvement	8
	Polyploidization and the Evolution of Spinnable Fiber	9
	Interspecific Hybridization and Gene Introgression	12
	Gene Introgression in Feral and Landrace Populations	15
	Developmental Introgressive Breeding	17
	Summary	20
	References	20
2.	Allopolyploidy and Interspecific Hybridization for	
	Wheat Improvement	27
	Abstract	27
	Introduction	28
	Interspecific Hybridization and Allopolyploidy in Triticeae	28
	Allopolyploidy and Genome Clusters	28
	Hybridization and Introgression	30
	Hybridization and Genome Rearrangement	31
	The Contribution of Interspecific Hybridization and	
	Allopolyploidy to Common Wheat Genome Formation	32
	Common Wheat Resulted from Multiple Rounds of Interspecific	
	Hybrid Speciation	32
	Regional Subgenome Expression Level Dominance in	
	Common Wheat	33
	Natural Introgression Between Common Wheat and	
	Other Species	34

	interspecific Manipulation of Genetic Recombination for	
	Wheat Improvement	35
	Gene Transfer from Donor Species of Wheat by Homologous	
	Recombination	35
	Gene Transfer from Alien Species into Wheat by	00
	Non-Homologous Recombination	38
	Interspecific Manipulation of Ploidy for Wheat Improvement	42
	Uniparent Genome Elimination Post-Pollination	42
	Genome Doubling by F <sub>1</sub> Hybrid Plants	43
	Single Genome Elimination During Hybrid Selfing	44
	Conclusions	45
	Acknowledgements	46
	References	46
3.	Potato Breeding through Ploidy Manipulations	<b>54</b>
	Abstract	54
	Introduction	54
	Potato Relatives and Significant Reproductive Characteristics	57
	Breeding Objectives	62
	Development of Ploidy Series	63
	The Monoploid Level $(2n = x = 12)$	64
	The Diploid Level $(2n = 2x = 24)$	65
	The Triploid Level $(2n = 3x = 36)$	67
	The Tetraploid Level $(2n = 4x = 48)$	67
	The Pentaploid $(2n = 5x = 60)$ and Hexaploid $(2n = 6x = 72)$ Levels	70
	The Molecular Breeding Perspective	70
	References	72
4.	Polyploid Induction Techniques and Breeding	,
	Strategies in Poplar	76
	Abstract	76
	Introduction	76
	The Advantages and Applications of Allotriploids in the	70
		77
	Genetic Improvement of Poplar  The Mainways and Mathada for Polarida Poplar Production	
	The Mainways and Methods for Polyploid Poplar Production	79
	Triploid Poplar Breeding by Hybridizing with	00
	Spontaneous 2n Gametes	80
	Triploid Poplar Breeding by Crossing with Artificial 2 <i>n</i> Pollen	82
	Triploid Poplar Breeding by Megaspore Chromosome Doubling	84
	Triploid Poplar Breeding by Embryo Sac Chromosome Doubling	86
	Tetraploid Poplar Breeding by Zygote or Somatic Cell	Charles I
	Chromosome Doubling	87
	Important Aspects of Chromosome Doubling and	
	Polyploidy Breeding in Poplar	89
	Knowledge of Reproductive Biology Characteristics is the	
	Key to Improving Chromosome Doubling Efficiency in Poplar	89
	The Utilization of Heterozygosity in Poplar Polyploidy Breeding	
	Should Attract More Attention	90

Will Guarantee Success in Poplar Polyploid Breeding References  Musa Interspecific Hybridization and Polyploidy for Breeding Banana and Plantain (Musaceae) Abstract Introduction  Musa Diversity and Banana/Plantain Cultigen Pools Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials  Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	92 93 97 98 98 100 101 103 103 104 106 106 106
Musa Interspecific Hybridization and Polyploidy for Breeding Banana and Plantain (Musaceae) Abstract Introduction Musa Diversity and Banana/Plantain Cultigen Pools Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	97 98 98 100 101 103 103 104 106 106
Abstract Introduction Musa Diversity and Banana/Plantain Cultigen Pools Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	97 98 98 100 101 103 103 104 106 106
Abstract Introduction Musa Diversity and Banana/Plantain Cultigen Pools Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	97 98 98 100 101 103 103 104 106 106
Introduction  Musa Diversity and Banana/Plantain Cultigen Pools  Sources of Variation  Interspecific Hybridization and Ploidy Manipulations  From Hybrid Seedlings to On-Station Field Testing  Target Traits  Crossbreeding  Field Plot Techniques  On-Station Trials  Multi-Environment Trials, Cultivar Development and Delivery  Multi-Environment Trials	98 98 100 101 103 103 104 106 106
Musa Diversity and Banana/Plantain Cultigen Pools Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	98 100 101 103 103 104 106 106
Sources of Variation Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	100 101 103 103 103 104 106
Interspecific Hybridization and Ploidy Manipulations From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	101 103 103 103 104 106 106
From Hybrid Seedlings to On-Station Field Testing Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	103 103 103 104 106 106
Target Traits Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	103 103 104 106 106
Crossbreeding Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	103 104 106 106
Field Plot Techniques On-Station Trials Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	104 106 106
On-Station Trials  Multi-Environment Trials, Cultivar Development and Delivery  Multi-Environment Trials	106 106
Multi-Environment Trials, Cultivar Development and Delivery Multi-Environment Trials	106
Multi-Environment Trials	
	106
Bred-Germplasm Releases	107
Delivering Bred-Germplasm	109
Quantitative Genetics, Genomics and Musa Breeding	109
DNA Marker-Aided Breeding	110
References	111
Strawberry (Plants in the Genus Fragaria)	115
Abstract	115
Introduction	115
	116
1 0,	116
	117
	119
· · · · · · · · · · · · · · · · · · ·	120
	122
	132
	132 133
	134
	134
	134
	138
	138
	141
	142
	142
	146
Interenacific Hybrid (10x) Cultivar 'Tokun' in Japan	
Interspecific Hybrid (10 <i>x</i> ) Cultivar "Tokun" in Japan Conclusions	151
	Basic Information for Species and Interspecific Hybrids in Genus Fragaria Morphology of the Plants in the Genus Fragaria Species in the Genus Fragaria Interspecific Hybrids in Nature Relatedness Between Species Breeding Using Interspecific and Intergeneric Hybrids in Genus Fragaria Breeding of 8x F. × ananassa Using Wild 8x Octoploids Breeding of 8x and 10x Cultivars Using Non-8x Wild Species Breeding Using Intergeneric Hybrids Practical Methods of Breeding Using Interspecific Hybrids Methods to Evaluate Hybridity and the Effect of Chromosome Doubling Treatments Chromosome Observations Flow Cytometry Analysis DNA Analysis Recent Progress of our Breeding Program Using the Decaploid Interspecific Hybrid (10x) Cultivar 'Tokun' in Japan

7.	The Role of Polyploidization and Interspecific Hybridization	
	in the Breeding of Ornamental Crops	159
	Abstract	159
	Introduction	159
	Mode of Origin of Polyploids	160
	The Origin of 2n Gametes	161
	Interploidy Crosses	164
	Lilium	165
	Classification and Main Cultivated Groups	165
	Ploidy Level of Species	165
	Polyploidization in Lilies	165
	Genome Differentiation Based on GISH Analysis	166
	Tulipa	167
	Systematic, Species and Main Cultivated Groups in the	
	Genus <i>Tulipa</i>	167
	The Main Goals of Tulip Breeding	168
	Chromosome Numbers of <i>Tulipa</i> Species and Varieties	168
	Polyploidization in Tulips	168
	Cytogenetic Analysis in Genus Tulipa	170
	Begonia	171
	Distribution and Classification	171
	The Main Cultivated Groups	171
	Breeding Objectives	172
	Basic Chromosome Number and Karyology of Begonias	173
	Genome Differentiation by GISH	173
	Unreduced Gametes	174
	Narcissus	174
	Cytological Analysis in Narcissus	175
	Conclusions	175
	References	176
8.	Polyploidy in Maize: The Impact of Homozygosity and	
	Hybridity on Phenotype	182
	Abstract	182
	Introduction	182
	Hybridity and Ploidy	185
	Why Not Double Cross Tetraploid Maize in the Field?	186
	Inbreeding Depression in Diploid and Tetraploid Maize	187
	What does the Behavior of Hybrid Polyploids Contribute to an	
	Understanding of Heterosis?	188
	Dosage Component of Polyploidy Heterosis	189
	Is there a Future for Polyploidy in Maize Cultivation?	189
	References	189
9.	Broadening the Genetic Basis for Crop Improvement: Interspecific	
	Hybridization Within and Between Ploidy Levels in Helianthus	192
	Abstract	192

	Introduction	192
	Plant Genetic Resources: Crop Wild Relatives	192
	Definitions	193
	Sunflower Domestication and Improvement	194
	Domestication and Improvement of Jerusalem Artichoke	196
	Gene Flow Between Wild and Cultivated Populations	196
	How Can We Utilize Hybridization Within Helianthus?	197
	Hybridization in Nature	197
,	Chromosomal Compatibility Within the Genus	198
	General Utility of Helianthus Crop Wild Relatives	200
	Cytoplasmic Male Sterility and the Formation of a Hybrid	
	Seed Industry	200
	Introgression of Disease Resistance	204
	Crosses Between the Crops: Interspecific Hybridization	
	Between H. tuberosus and H. annuus	205
	New Tools for Easier Use of Wild Relatives	206
	Next Generation Germplasm Resources	207
	Conclusions	207
	References	208
10.	Crop Improvement of Phaseolus spp. Through Interspecific and	
	Intraspecific Hybridization	218
	Abstract	218
	Introduction	218
	Origin, Domestication and Expansion of Phaseolus Crop Species	219
	Evolution for Breeding	225
	Intraspecific and Interspecific Hybridization in Phaseolus Species	226
	Biotic Stress	228
	Fungal Pathogens	229
	Bacterial Pathogens	236
	Viral Pathogens	238
	Insects and Nematodes	240
	Abiotic Stress	241
	Drought	242
	Heat and Cold	245
	Phosphorus Availability	247
	Nitrogen Fixation	248
	Aluminum Tolerance	250
	Yield	252
	Nutritional Quality	254
	Proteins and Anti-Nutritional Compounds	254
	Micronutrients	257
	Conclusions	259
	References	260
11.	Triticale	283
	Abstract	28

	Introduction		281
	Ploidy Levels and Chromosome Constitutions		284
	Triticale Breeding		290
	Frost Resistance		293
	Lodging Resistance		294
	Pre-Harvest Sprouting		294
	Fungal Diseases		295
	Aluminium Tolerance		295
	Hybrid Triticale		296
	Doubled Haploids of Triticale		298
	Utilization of Triticale		304
	Recent Developments		305
	Acknowledgements		307
	References		307
12	Polyploidy and Interspecific Hybridization in Cy	nodon	307
14.	Paspalum, Pennisetum, and Zoysia	nouon,	318
	Abstract		318
	Introduction		318
	Cynodon Germplasm		319
	Turf Hybrids		319
	Forage Hybrids		320
	Pennisetum Germplasm		320
	Interspecific Forage Hybrids		321
	Trispecific Ornamental Hybrids		321
	Genome (or Partial) Transfer		322
	New Stable Cytoplasm		322
	Transfer of Apomixis		323
	Paspalum Germplasm		324
	Dallisgrass Phylogenetics		324
	Bahiagrass and Other <i>Paspalum</i> Species		328
	Polyploidization		329
	Zoysia		330
	Summary		333
	References		334
12	Interploid and Interspecific Hybridization for		334
13.	Kiwifruit Improvement		339
	Abstract		339
	Introduction		340
	Breeding Aims		340
	The Genus Actinidia		341
	Actinidia Species		343
	1	one	343
	Ploidy and Ploidy Races in Wild <i>Actinidia</i> Population Basic Chromosome Number	1118	343
	Ploidy Races in <i>Actinidia</i>		344
			344
	Ploidy Races in the Actinidia arguta Complex		044

	Ploidy Races in the Actinidia chinensis Species Complex	345
	The Need to Check the Ploidy of Individual Genotypes	346
	Interspecific and Interploidy Actinidia Hybrids in Nature	346
	Controlled Crossing and Introgression in Actinidia	347
	Pollenizer Ploidy	350
	Manipulation of Ploidy in Actinidia	350
	Chromosome Doubling	351
	Unreduced Gametes	351
	Production of Haploids	352
	Endosperm Culture	352
	Protoplast Fusion	352
	Cultivars Resulting from Interspecific or Interploidy Crosses	353
	Future Prospects	354
	Acknowledgements	355
	References	355
14.	Oat Improvement and Innovation Using Wild Genetic Resources	
	(Poaceae, Avena spp.): Elevating "Oats" to a New Level and	
	Stature	364
	Abstract	364
	Introduction	365
	Obstacles to Transformational Improvement of the	
	Hexaploid Oat Gene Pool	367
	Hexaploid Oat Production and Climate Change	367
	Exotic Major Oat Resistance Genes, Durability, and	
	Linkage Drag	368
	Impact of Genomic Buffering on Breeding Progress	370
	Specialized Interploidy Avena Breeding Efforts	370
	Domestication of Avena magna	370
	Synthetic Polyploids: Amagalon, Strimagdo, Macrosativa, etc.	371
	Improvement of A,A, Diploid Oat	372
	Variation and Potential of the A. strigosa Biological	
	Species Group	372
	Conclusion	373
	References	373
15.	Interspecific Hybridization of Chestnut	377
	Abstract	378
	Introduction	378
	Chestnut Germplasm	379
	Genomic Resources for Castanea	379
	Development of Molecular Markers	380
	Genome-Wide Selection for Advancing Introgression Breeding	383
	Genetic Diversity Within the Genus Castanea	384
	Genetic Diversity Within Chinese Chestnut: C. mollissima	385
	Genetic Diversity Within North American Species C. dentata,	
	C. pumila and C. ozarkensis	386

	Genetic Diversity Within European Chestnut C. sativa	386
	Genetic Diversity in Japanese Chestnut C. crenata	388
	Mating System in Castanea	389
	Hybridisation Between Species	390
	Cross-Pollination to Produce Interspecific Hybrids	390
	Interspecific Hybridisation for Chestnut Improvement	391
	Interspecific Hybridization to Introgress Disease and	
	Insect Resistance into European Cultivars	391
	Complex Interspecific Hybridisation for Multiple Trait	
	Improvement in Turkey	394
	Introgressing Resistance to Chestnut Blight in the USA	395
	Interspecific Hybridisation for Chestnut Improvement in Japan:	
	Easy-Peeling Pellicles	396
	Interspecific Hybrid Mapping Populations	398
	Conclusions	398
	Acknowledgements	399
	References	399
16.	Use of Polyploids, Interspecific, and Intergeneric Wide Hybrids	
	in Sugar Beet Improvement	408
	Abstract	408
	Introduction	408
	Hybrids Using Patellifolia Species (Formerly Beta Sect.	
	Procumbentes)	411
	Hybrids Using Beta Sect. Corollinae	414
	Hybrids Using Beta Sect. Beta	415
	Future Considerations	416
	References	416
17.	Polyploidy in Watermelon	421
	Abstract	421
	Introduction	422
	Origin and Distribution of Watermelon	422
	Classification of Watermelon	422
	Triploid Seedless Watermelon	423
	The Cultivated Area of Triploid Watermelon	423
	The Cultivars of Triploid Watermelon	424
	The Advantages of Triploid Watermelon	424
	Tetraploid Watermelon Production	424
	Choice of Diploid Watermelon Lines	425
	Induction of Tetraploid Plants	425
	Identification of Tetraploid Plants	426
	Tetraploid Line Development	426
	Triploid Hybrid Production and Testing	427
	Triploid Watermelon Evaluation	427
	Evaluation of Triploid Hybrids	427
	Cultivation of Triploid Seedless Watermelon	428

		Contents	XV
	Future Possibilities for Polyploid Watermelon Improveme	nt	429
	References		429
18.	Optimization of Recombination in Interspecific Hybrid	s to	
	Introduce New Genetic Diversity into Oilseed Rape		
	(Brassica napus L.)		431
	Abstract		431
	Introduction		432
	Optimal Use of Homologous Recombination in		
	Interspecific Hybrids	den	434
	Optimal Use of Homeologous Recombination in		
	Interspecific Hybrids		436
	Conclusions		439
	Acknowledgements		441
	References		441
19.	Interspecific Hybridization for Chickpea (Cicer arietinu	m L.)	
	Improvement		445
	Abstract		445
	Introduction		446
	Taxonomical Relationship and Genepool in Genus Cicer		448
	Wild Cicer Species as a Source of New Variability		454
	Limitations of Utilizing Wild Cicer Species for Chickpea		
	Improvement		454
	Pre-breeding for Broadening the Genetic Base of Chickpe	a	455
	Global Success Stories of Utilizing Wild Cicer Species for	or	
	Chickpea Improvement		455
	Achievements and Present Status at ICRISAT		456
	Genomic Resources for Chickpea Improvement		459
	Future Strategies		463
	References		464

Index

# Interspecific Hybridization for Upland Cotton Improvement

Peng W. Chee<sup>1,\*</sup>, Andrew H. Paterson<sup>2</sup>, Joshua A. Udall<sup>3</sup> and Jonathan F. Wendel<sup>4</sup>

#### ABSTRACT

Interspecific hybridization has been central to the evolution, domestication, and improvement of Upland cotton, the cultivated form of Gossypium hirsutum. As the world's most important fiber crop species, Gossypium hirsutum belongs to the allotetraploid Gossypium clade that consists of six additional species. The lint fiber evolved only once in the history of Gossypium, in the ancestor diploid A-genome species, and this trait was passed on to the allopolyploid species when the A-genome united in a common nucleus with a D-genome from the other ancestor that produced no lint fibers. The domestication history of G. hirsutum involved the collection and use of lint fibers by indigenous people for the purpose of making strings and other textile products; hence, spinnable lint fibers were likely to have evolved under domestication. The geographical distribution of G. hirsutum overlaps with G. barbadense and G. mustelinum, and gene flow among these species has been documented. Therefore, the introgression of novel alleles into G. hirsutum possibly contributed to greater ecological adaptation in colonizing new habitats and providing important sources of genetic variation for artificial selection in the early domestication efforts. In modern Upland cotton, numerous germplasm lines have been developed from crossing with G. barbadense. However, reproductive barriers such as reduced fertility, segregation distortion, and hybrid breakdown are often observed in later

E-mail: jaudall@byu.edu

<sup>&</sup>lt;sup>1</sup> Institute of Plant Breeding, Genetics, and Genomics, University of Georgia – Tifton Campus, Tifton, GA 31794, USA, E-mail: pwchee@uga.edu

<sup>&</sup>lt;sup>2</sup> Plant Genome Mapping Laboratory, University of Georgia, Athens, GA 30602, USA, E-mail: paterson@uga.edu
<sup>3</sup> Department of Plant and Wildlife Science, Brigham Young University, Provo, Utah, USA,

<sup>&</sup>lt;sup>4</sup> Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA, E-mail: jfw@iastate.edu

<sup>\*</sup> Corresponding author

generation hybrids between *G. hirsutum* and the other polyploid species, complicating the task of introgressing new, stably inherited allelic variation from inter specific hybridization. Recent efforts in molecular genetic research have provided insights into the location and effects of QTLs from wild species that are associated with traits important to cotton production. These and future research efforts will undoubtedly provide the tools that can be utilized by plant breeders to access novel genes from wild and domesticated allotetraploid *Gossypium* for Upland cotton improvement.

#### **The Cotton Crop**

The cotton plant is a source of both food and fiber, contributing to two basic needs of humanity. Cotton fiber in the form of textile products has contributed greatly to the comfort, style, and culture of human society. Although not commonly viewed as a food source, cotton is an important source of vegetable oil used extensively in foodstuffs such as baking and frying fats, mayonnaise, margarine, and snack food. Furthermore, after oil extraction, the seed by-product is used as raw material in livestock feed, fertilizer, and paper. This versatility has made cotton one of the most important field crops in the world.

According to the International Cotton Advisory Committee (ICAC), which collects statistics on world cotton production, consumption and trade, about 36 million hectares of cotton are planted in over 100 countries from latitudes 45°N in Ukraine to 32°S in Australia (ICAC, 2015). The top five cotton producing countries in the 2014-15 season include, in order of importance, China, India, the United States, Pakistan and Brazil, which collectively account for nearly two-thirds of the world's cotton production. Total cotton fiber production has now reached 106 million bales, and contributes about 40% of the world fiber market (ICAC, 2015), thus making cotton the single most important natural fiber in the textile industries and a vital agricultural commodity in the global economy. The aggregate value of the world's cotton crop is estimated to be about US\$30 billion/vr, with 90% of its value residing in lint fiber. More than 350 million people are engaged in jobs related to the production and processing of cotton. The economic importance of cotton as a natural fiber for the global textile industry has fueled considerable interest in improving the inherent genetic potential of the crop through breeding for cultivars with higher levels of biotic and abiotic tolerance as well as higher lint yield and the further enhancement of fiber quality.

Interspecific hybridization has been central to the evolution of cotton, and to its improvement. As a crop, cotton is unique in that four different species in the genus *Gossypium* (Malvaceae) were domesticated independently on two separate continents for lint fiber production (Wendel and Cronn 2003; Wendel and Grover 2015). Therefore, the word "cotton" in the textile industry can apply equally to the two allotetraploid species *G. hirsutum* L. and *G. barbadense* L., endemic to the Americas, and the two diploid species