# FLOWER BREEDING AND GENETICS

# Flower Breeding and Genetics

## Issues, Challenges and Opportunities for the 21st Century

*Edited by*

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Caption of cover illustration:
Wildflowers of the Carizzo Plains (San Luis Obispo County, California, U.S.A.) burst into bloom after heavy winter rains in Spring, 2005. This photo illustrates the many wild, flowering species across the globe which have yet to be collected, bred, and domesticated as flowering crops.

Photo Credit: Jean Gordon, Jeff Gordon (San Luis Obispo, California, U.S.A.)

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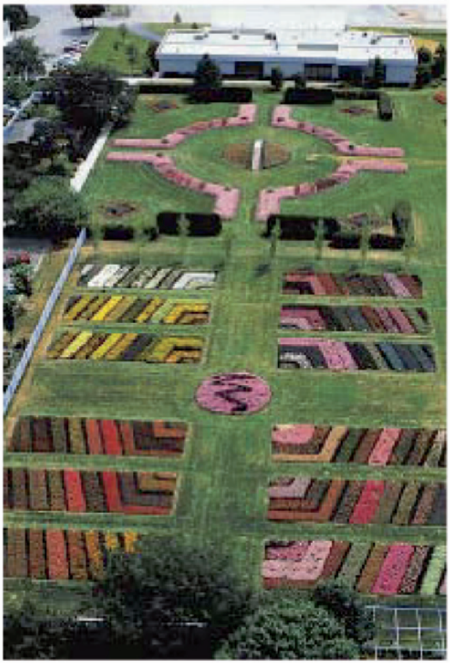

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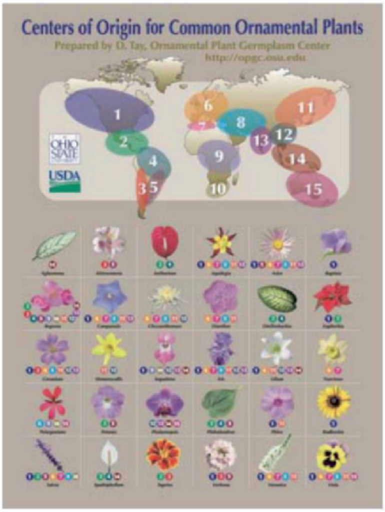


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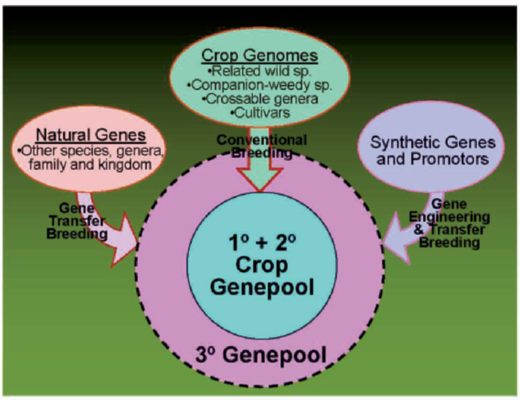


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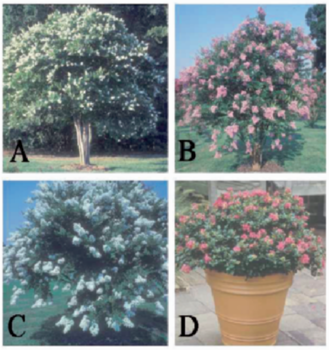

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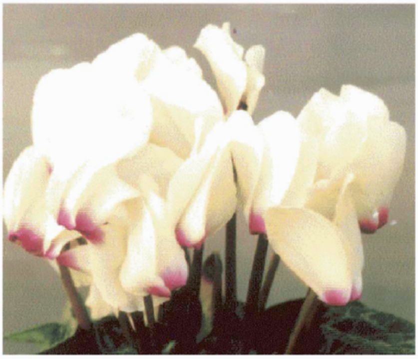
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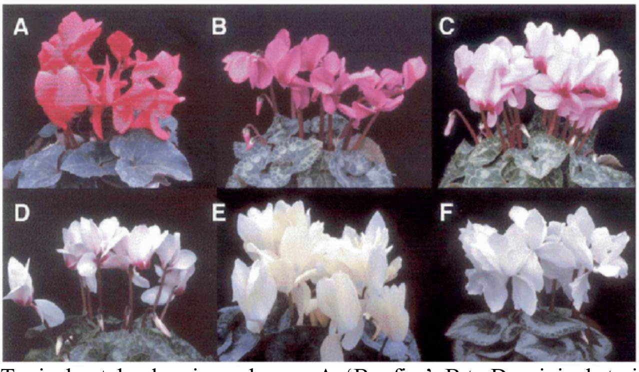

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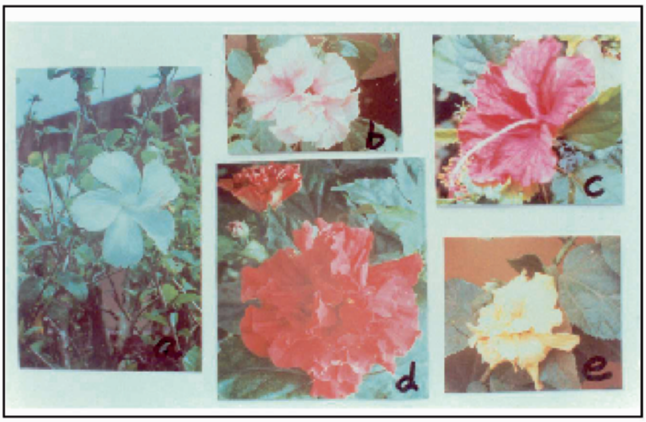


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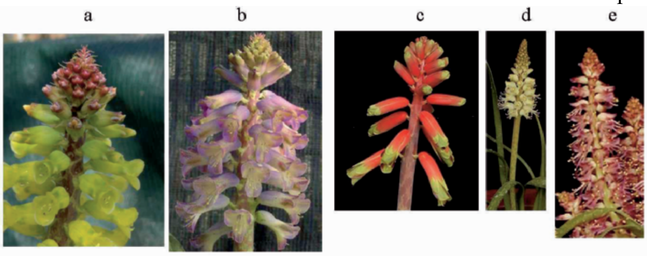


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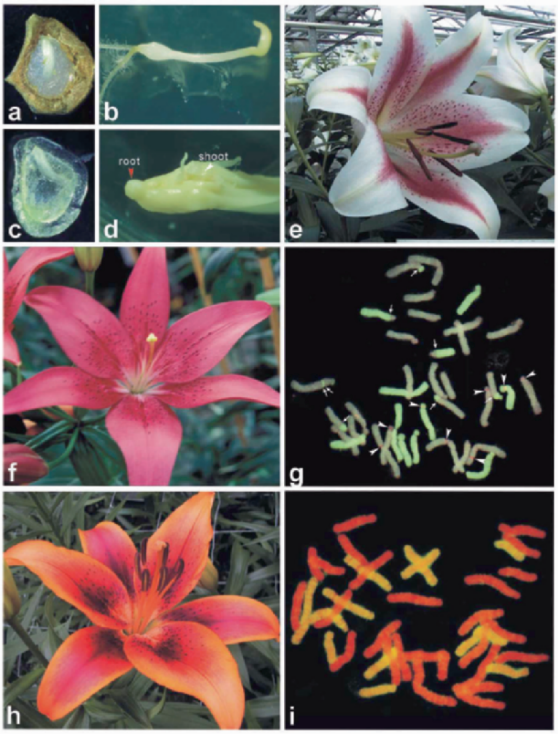


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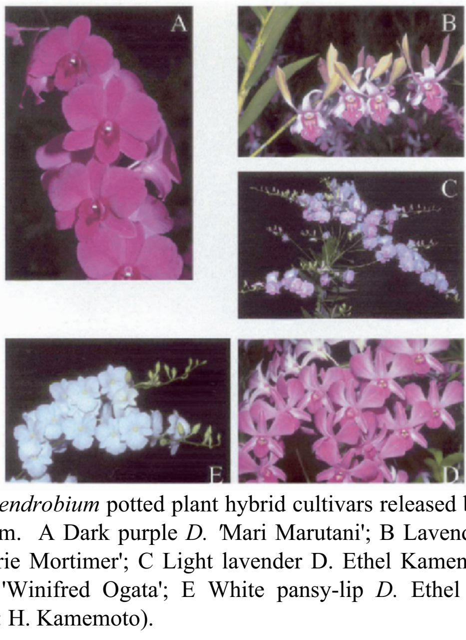


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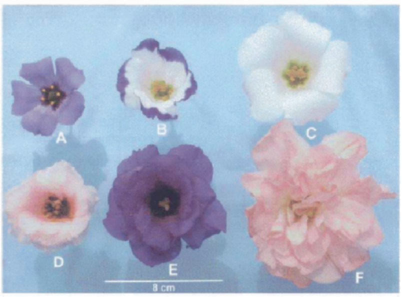


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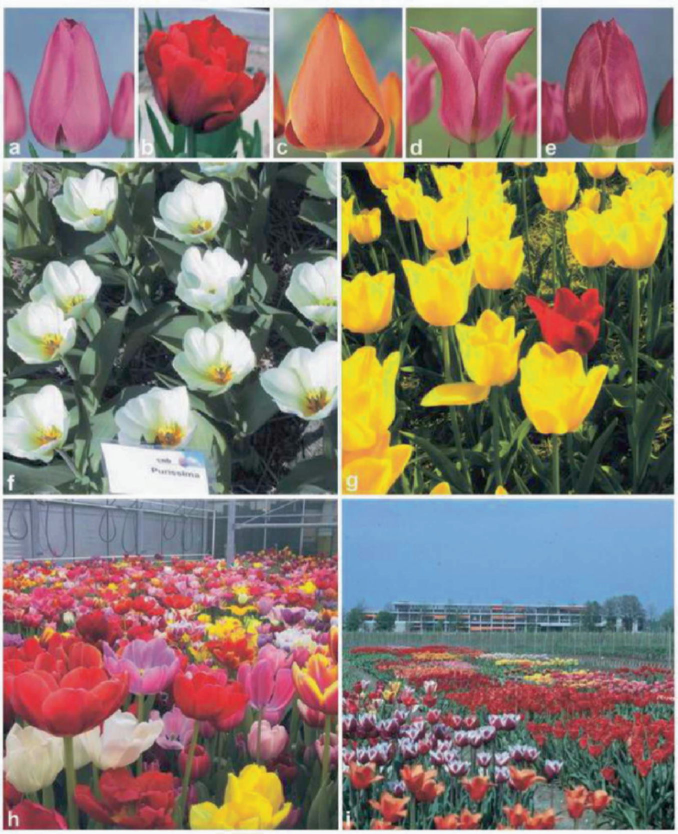

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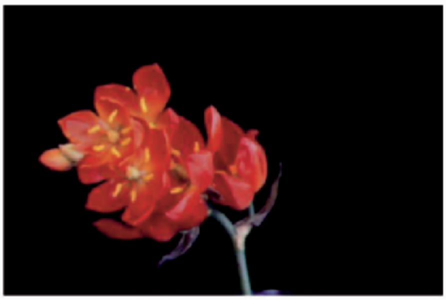

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# PART I

# FLOWER BREEDING PROGRAM ISSUES

# Introduction

## FLOWER BREEDING & GENETICS
*Issues, challenges, and opportunities for the 21st Century*

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Flowers have long been associated with each civilization and culture in the world. Dating as far back as the Neanderthals, flowers were used to decorate graves and celebrate major life events, expressing emotions in ways that words are deficient. Numerous cultures have incorporated flowers into their everyday lives as expressions of beauty and art. The first flower breeder is unknown, but the historic record provides us with a rich accounting of numerous flower selections and cultivars, presumably many of which were either selected as mutations or the result of directed breeding. Many seed and vegetatively-propagated cultivars of flower crops have been preserved as heirlooms, landraces, and are important sources of historic germplasm.

The science and art of flower breeding and genetics is not well documented. Much of the knowledge is transferred from one generation of flower breeders to the next within each public and private sector breeding program. While there are many monographs devoted to specific crops, few, if any, attempt to combine a diverse array of floriculture crops and address important issues for the current and following generations of flower breeders/geneticists. Oddly enough, the early genetics work of the $20^{th}$ century (e.g. research by East, Mangelsdorf, etc.) was conducted on flowering crops, such as snapdragons and flowering tobacco. Unfortunately, subsequent genetic research often shifted to agronomic (food) crops. Flower breeders, while hard at work researching, collecting wild germplasm, domesticating seed and vegetative crops, and producing thousands of new cultivars for the commercial market, remained predominantly beneath the radar screen. As a result, our current floricultural crops have a paucity of genetic and breeding data in the public record since most of the last



*N.O. Anderson (ed.), Flower Breeding and Genetics*, 3–5.

century's efforts are proprietary in the private breeder companies. A recent publication on Flower Seeds (edited by McDonald and Kwong, CABI publishers, 2004) has helped to change this dilemma. This monograph is dedicated to alleviating this oversight with the goal of preserving much of the genetic and breeding information for future use, as well as spawning the domestication of future floricultural crops.

It was under this pretext that the present monograph was conceptualized by many members of the Ornamental Plant Breeding Working Group, under the auspices of the American Society of Horticultural Scientists. Additional ideas and input arose from discussions with other scientists at the annual meetings of the International Society for Horticultural Science. Undoubtedly, the primary reason no previous monograph has been devoted to such a wide range of topics as are covered in this book is that it is a monumental task. I was eager to assume editorship of this monograph, having directed both private and public sector flower breeding programs, as I felt there was a profound need for such a reference. The call for submissions began in 2001; reviewing and final editing took four years to accomplish due to the scope of topics and crops covered, as well as the busy schedules of each and every contributor.

This book has many significant contributions to the science of flower breeding and genetics. The first six chapters are devoted to topics of wide interest to floriculturists and all plant breeders. Dr. John Erwin provides a thorough examination of the factors affecting flowering in Chapter 1. The essential elements of flowering need adequate characterization and manipulation for any flowering crop to be successfully bred, domesticated, and introduced into the market. Advent of new traits in floriculture crops are explored in many chapters, including the phenomenon of 'annualized perennials' by Drs. Wilkins and Anderson (Chapter 2). The science and art of cultivar trialing in private and sector breeder trials and display gardens is exquisitely delineated by the foremost trial coordinator of our time, Mr. Jim Nau of Ball Horticultural Company (Chapter 3). Marketing of floriculture crops is probably the most advanced of any horticulture or agronomic commodity and can serve as a template for many other crops. Ms. Penny Aguirre provides detailed explanation of all the necessary protection, which can be offered to new flower products in any country of the world (Chapter 4). Never before have we had the opportunity to have a reference devoted to plant germplasm collection, maintenance, and the necessary rules of adherence to international and national treaties governing plant germplasm. Dr. David Tay, the Director of the Ornamental Plant Germplasm Center for the United States Department of Agriculture, provides an exhaustive description of important procedures on this topic (Chapter 5). New issues continually face the global floriculture market, not least of which is crop invasiveness. Dr. Anderson brings this topic to the attention of our readers to encourage flower breeding programs and all other parties in the distribution channel to research and develop strategies to prevent continued release of invasive flowering crops (Chapter 6).

The sections of crop-specific breeding & genetics are divided into four floriculture commodity groups: bedding plants, flowering potted plants, cut flowers, and herbaceous perennials. Breeding and genetic techniques for a total of 24 floriculture crops are covered in these sections. Insertion of each crop into one of these commodity groups was a challenge, since many crops are in multiple groups. I chose to insert each crop into a commodity grouping, based on its predominant use in the marketplace. Chapter formats for each crop follow a similar layout for ease in reading.

The crops covered in these sections represent a diversity of life history (annual—perennial), age (new—old crops), levels of domestication (relatively recent to those >1,000 years old), ploidy (diploid to complex polyploids), breeding systems (self incompatible to self compatible and all combinations in between), propagation mode (seed, vegetative), etc. Many crops have relatively little genetic information available. We look to future generations of flower breeders/geneticists to expand this area. Other crops require other research topics to be addressed, such as linkage maps, trisomic development, genetic engineering, regeneration/transformation technologies, shortening lengthy life cycles, cytogenetics, manipulation of ploidy levels, interspecific hybridization, removal of reproductive barriers, manipulation of hybrid breakdown, etc. Each author provides an extensive review of the literature, the current state-of-the-art, crop-specific future needs, and ideotypes for continued transformation of each taxa.

I trust that each reader will use the information contained herein to further the progress in flowering crops for future generations. Flower breeding & genetics is an exciting field of research and discovery. Numerous scientists have devoted their lives to this subject. It is one of the most rewarding professions in the world!

Neil O. Anderson, Editor
15 September 2005

Chapter 1

# FACTORS AFFECTING FLOWERING IN ORNAMENTAL PLANTS

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Abstract: Flowering is the cornerstone of floricultural crops, regardless of class (bedding plants, herbaceous perennials, cut flowers, flowering potted plants); the only crop exceptions are those grown for their colorful foliage. During flower breeding and crop domestication, both public and private sector flower breeding programs must conduct research to discern the various control mechanisms for flower initiation and development. Important flowering concepts covered in this chapter include autonomous regulation (phase change; species, meristem size, and environmental factor affects), external regulation (photoperiodism, vernalization, devernalization, irradiance and light quality, and their interactions), irradiance induction, stress induction (ehtylene, water), flower development requirements (photoperiodism, temperature, stress), and dormancy.

Key words: Dormancy, facultative irradiance response, floral evocation, floral induction, flower initiation, flower development, heat delay, irradiance indifference, phase change, plant growth regulators, vernalization.

## 1. INTRODUCTION

Flowering, or the transition from leaf (vegetative phase) to flower (reproductive phase) production by a meristem, can be stimulated by internal or external cues. Internal or autonomous cues include flowering responses that result from factors such as plant age or size. In contrast, external cues include flowering responses that result from environmental stimuli such as day/night length, low temperature, fire, and/or the presence of water. The development of internal cues to control flowering enable plants to regulate flowering when a plant is at an optimal size or age. The



*N.O. Anderson (ed.), Flower Breeding and Genetics*, 7–48.

development of external cues allows for optimal timing of flowering during a year to ensure successful pollination and seed development prior to inclement conditions as well as for synchronized flowering within a population. Such synchrony is essential to for successful cross-pollination of outcrossing species.

Steps in the flowering process, as well as autonomous and external cues that result in flowering and how they can be applied by flower breeders / plant physiologists will be discussed in this chapter. Both basic and applied literature will be reviewed. The chapter will distinguish between factors that result in flowering as a result of induction versus the breaking of dormancy. In addition, detailed information on specific conditions that promote flowering of a number of herbaceous ornamental species will be presented to enable a commercial grower, private or public sector flower breeder, and/or research scientist to induce flowering at any desired time. Much of this specific information is very recently discovered. In addition, data on classification of species into irradiance response groups has recently been introduced (Erwin and Warner, 2002; Mattson, 2002; Mattson and Erwin, 2003 a, b).

# 2. THE FLOWERING PROCESS

## 2.1 Terminology

The processes whereby events in a shoot meristem are altered in such a way to produce flowers as opposed to leaves are collectively referred to as '**floral evocation**'. '**Floral induction**' is the actual signal that results in evocation. Formation of flower buds after induction is referred to as '**flower initiation**'. The process after flower initiation until anthesis is referred to as '**flower development**'. '**Anthesis**' refers to the shedding of pollen by the stamen. It should be noted that flower opening (petal unfolding) can occur prior to, during, or after anthesis.

A meristem is '**competent**' to flower when it can respond, in the expected manner, when given an appropriate developmental signal. Such a meristem is referred to as '**determined**', if it follows the same developmental program even after it is removed from a source of environmental or biochemical stimulus. In some cases the '**expression**' of flowering can be delayed until a second developmental signal is received. For instance, some species require a succession of two different photoperiods for successful evocation. Similarly, some species require a cold temperature treatment followed by a specific photoperiod for successful evocation.

Often, floral induction and flower initiation have occurred, but flower development is interrupted. Such a suspension in flower development is, in some cases, referred to as '**dormancy**'. In most cases, a single or series of environmental cues must occur for dormancy to be broken. Dormancy is common for flowering in spring-flowering woody species and ephemerals.

The complexity of control mechanisms associated with flowering is enormous. It is amazing that flowering can occur at all, given the sensitivity of each step and the possibility for interruption during the flowering process which is significant. If a single factor is promotive, it is possible for flowering to be inhibited if other conditions are not met. Yet, plants have a significant redundancy incorporated into the flowering process to ensure that a number of cues can enable flowering to compensate for environmental fluctuations. The inherent redundancy in the flowering system as well as ways in which several environmental cues can result in the same flower induction is apparent in recent models.

## 2.2 Autonomous Regulation of Flowering

Organisms pass through a series of developmental phases during growth and maturation. Among animal species, developmental phase changes are ubiquitous throughout the organism. In contrast, among plants such phase changes take place only in the shoot apical meristem; flowering is only possible if a meristem is competent to flower and it receives an inductive signal.

Whether a meristem is competent to flower is dependent on the phase, which the meristem is in. The transition between phases in development is referred to as '**phase change**'. A plant passes through three phases: the juvenile, adult vegetative (competent), and adult reproductive (determined) phases. The critical difference between the juvenile and adult phases is inherent in the ability of that meristem to successfully flower, which is only observed in the adult phases. The critical difference between the adult vegetative and adult reproductive phases are simply whether that meristem has or has not been evoked to flower or is determined.

Whether a plant is competent or determined with respect to flowering can be evaluated using grafting experiments (McDaniel, et al., 1992). If a non-flowering scion is grafted onto an induced rootstock and the scion flowers, then the scion must have been competent to respond to the floral stimulus. In contrast, if the scion does not flower, it is not yet competent. If a scion is grafted onto a juvenile rootstock and the scion flowers regardless, it is likely to be determined. For instance, *Betula verrucosa* J.F. Ehrh. tissues derived from the base of the tree (juvenile) grafted onto a rootstock remain juvenile or vegetative, i.e. the scion was not competent to flower (Longman, 1976). In contrast, plant tissues collected from the top of the flowering tree (mature) were competent to flower after two years.

It must be emphasized that the transition from juvenile to adult phases is a continuous process and not discontinuous. For instance, the ability to flower is a process and is transitional. *Lunaria biennis* L. (Wellensiek, 1958), *Brassica oleracea var. gemmifera* (Stokes and Verkerk, 1951), and *Beta vulgaris* (Wellensiek and Hakkaart, 1955) pass through a clear juvenile to adult phase transition, as