

The Global Flower Bulb Industry: Production, Utilization, Research

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LITERATURE CITED

I. INTRODUCTION

Flower bulbs, also called ornamental geophytes (Raunkiaer 1934; Rees 1989; Halevy 1990; De Hertogh and Le Nard 1993b), exhibit great diversity in their morphology, growth and developmental biology, and physiological responses to environmental factors. Horticulturally, they contribute significantly to the global ornamental industry, and are utilized for commercial bulb and flower production, including outdoor and forced fresh-cut flowers and potted plants, and for landscaping, including private gardening.

Although ornamental geophytes belong to more than 800 different genera, the industry is dominated by 7 genera: *Tulipa*, *Lilium*, *Narcissus*, *Gladiolus*, *Hyacinthus*, *Crocus*, and *Iris*. Most of the traditional flower bulbs are cultivated in temperate-climate regions of the world. However, as the global demand for all ornamental geophytes continues to increase, it is obvious that innovative production and marketing efforts are needed. This is true not only for the leading genera but also for the extensive diversity that exists among the several hundred other taxa (Bryan 1989, 2002). Thus, in a new production area with a warm climate, research needs to be focused primarily on the development of new commercial products and precision production methods. At the same time, special techniques must be developed for the successful production of the traditional taxa. Therefore, this chapter has three primary objectives: (1) to focus on the global status of the flower bulb industry; (2) to outline the salient scientific research that has led to the success of the industry and, especially, the studies that have been conducted in the past

100 years; and (3) to summarize the impact and roles of the commercial, hobbyist, and government organizational infrastructures that have and it is hoped will continue to support the flower bulb industry.

II. HISTORICAL PERSPECTIVES

Flower bulbs have been appreciated and cultivated for thousands of years and long before they were widely grown commercially or extensively researched. They are mentioned frequently in mythology, ancient history, art, and literature (Correvon and Massé 1905; Reynolds and Meachem 1967; Jefferson-Brown 1969; Doerflinger 1973; Genders 1973; Haw 1986; Scheider 1981; Todd and Penney 1994a,b; Pavord 1999; Baker et al. 1999; Ward 1999). In addition, species such as *Crocus sativus* (the saffron *Crocus*) were valued as spices and dyes, and some *Colchicum* and *Scilla* species were used in medicine. Binomials and authorities of all species mentioned in the text are presented in Table 1.1.

The introduction of the tulip to the Netherlands from Turkey, in the middle of the 16th century, was a key factor in the development of flower bulb industry in Europe and mainly in the Netherlands (Van der Sloot 1994; Pavord 1999). With the exception of *Narcissus*, all the major genera that contributed to the development of the bulb industry in the Netherlands (*Tulipa*, *Lilium*, *Gladiolus*, *Hyacinthus*, *Crocus*, and *Iris*) have been introduced to Europe. Thus the establishment and development of the flower bulb industry in the Netherlands over the last 400 years has occurred by adaptation of nonindigenous flower bulbs.

The diversification of the tulip occurred early in its culture. Three centuries before their introduction into Europe, tulips exhibited diversity in the Persian gardens (Botschantzeva 1982). In Turkey, tulip hybridization was active in the 16th through the 18th centuries, while in Western Europe, it started shortly after tulip introduction (Pavord 1999). By the end of the 17th century, hundreds of cultivars were available in France and in the Netherlands (De La Quintinye 1697; Pavord 1999). Some cultivars bred in the 18th or 19th century—for example, ‘Keizerskroon’ (1750) and ‘Couleur Cardinal’ (1845)—are still in commercial cultivation (Van Scheepen 1996; PT/BKD 2008).

Hyacinths were also introduced to the Netherlands in the middle of the 16th century. Their active hybridization started after 1700, and by the end of the 18th century, about 2,000 cultivars were grown (Doorenbos 1954). The major goal of the early hybridizations was to satisfy the requests of wealthy patrons who promoted bulb production and utilization. These individuals, through their influence on fashion trends, were able to affect

Table 1.1. Botanical names of the genera and species mentioned in the text.

<i>Agapanthus</i> L'Hér.	<i>Leucocoryne purpurea</i> Gay
<i>Agapanthus praecox</i> Willd.	<i>Leucojum aestivum</i> L.
<i>Allium</i> L.	<i>Liatris spicata</i> (L.) Willd.
<i>Alstroemeria</i> L.	<i>Liatris</i> Schreb.
<i>Anemone blanda</i> Schott & Kotschy	<i>Lilium auratum</i> Lindl.
<i>Anemone coronaria</i> L.	<i>Lilium bulbiferum</i> L.
<i>Anigozanthos</i> Labill.	<i>Lilium candidum</i> L.
<i>Aquilegia alpina</i> L.	<i>Lilium concolor</i> Salisb.
<i>Arisaema sikokianum</i> Franch & Sav.	<i>Lilium dauricum</i> Ker Gawl.
<i>Babiana</i> Sims	<i>Lilium japonicum</i> Thunb.
<i>Brodiaea</i> Sm.	<i>Lilium longiflorum</i> Thunb.
<i>Colchicum</i> L.	<i>Lilium maculatum</i> Thunb.
<i>Conanthera campanulata</i> Lindl.	<i>Lilium philippinense</i> Baker
<i>Conanthera trimaculata</i> F. Meigen	<i>Lilium rubellum</i> Baker
<i>Conanthera bifolia</i> Ruiz & Pav.	<i>Lilium speciosum</i> Thunb.
<i>Convallaria</i> L.	<i>Lilium tigrinum</i> Ker Gawl.
<i>Crocus sativus</i> L.	<i>Lilium</i> × <i>elegans</i> Thunb.
<i>Cyclamen</i> L.	<i>Muscari armeniacum</i> Baker
<i>Cyclamen persicum</i> Mill.	<i>Narcissus pseudonarcissus</i> L.
<i>Cyrtanthus</i> Aiton	<i>Narcissus tazetta</i> L.
<i>Dendrobium crumenatum</i> Sw.	<i>Nelumbo nucifera</i> Gaertn.
<i>Eucrosia</i> Ker Gawl.	<i>Neomarica</i> Sprague
<i>Eucharis amazonica</i> Linden	<i>Nerine</i> Herb.
<i>Freesia</i> Klatt	<i>Nerine bowdenii</i> W. Watson
<i>Fritillaria</i> L.	<i>Ornithogalum dubium</i> Houtt.
<i>Galanthus</i> L.	<i>Oxalis</i> L.
<i>Galtonia</i> Decne.	<i>Paeonia</i> L.
<i>Gladiolus</i> L.	<i>Pancratium</i> L.
<i>Gladiolus tristis</i> L.	<i>Pasithea caerulea</i> (Ruiz & Pav.) D. Don
<i>Gloriosa</i> L.	<i>Phalaenopsis equestris</i> (Schauer) Rchb.f.
<i>Gomphrena</i> L.	<i>Ranunculus asiaticus</i> L.
<i>Griffinia</i> Ker Gawl.	<i>Rhodophiala</i> C. Presl.
<i>Herbertia lahue</i> (Molina) Goldblatt	<i>Sandersonia</i> Hook
<i>Hippeastrum</i> Herb.	<i>Scilla</i> L.
<i>Hyacinthus orientalis</i> L.	<i>Sternbergia</i> Waldst. & Kit.
<i>Hyacinthus orientalis</i> var. <i>albulus</i> Baker	<i>Tulipa</i> L.
<i>Iris</i> L.	<i>Tulipa eichleri</i> Regel
<i>Iris</i> × <i>hollandica</i> hort.	<i>Tulipa fosteriana</i> Hoog ex W. Irving
<i>Iris reticulata</i> M. Bieb.	<i>Tulipa gesneriana</i> L.
<i>Ixia</i> L.	<i>Tulipa greigii</i> Regel
<i>Lachenalia</i> Murray	<i>Tulipa kaufmanniana</i> Regel
<i>Leontochir ovallei</i> Phil.	<i>Xiphium tingitanum</i> Mill.
<i>Leucocoryne</i> Lindl.	<i>Xiphium vulgare</i> Mill.
<i>Leucocoryne coquimbensis</i> F. Phil.	<i>Zantedeschia</i> Spreng.
<i>Leucocoryne coquimbensis alba</i> Zoellner	<i>Zantedeschia aethiopica</i> Spreng
<i>Leucocoryne ixioides</i> (Hook) Lindl.	<i>Zephyra elegans</i> D. Don

the development of new ornamental crops. For example, during the 17th century, the tulip dominated the hyacinth. However, after 1700, the hyacinth came into fashion; it was the queen of the bulb flowers until 1890, when the tulip regained its prominence (Doorenbos 1954).

During this period of breeding, no scientific database existed. This situation continued up to the 19th century, when narcissi and gladioli breeding programs were initiated (Wylie 1952; Fairchild 1953). Later, these breeding programs used the heredity characteristics proposed by Gregor Mendel in 1886 and the roles of the chromosomes, which that were discovered about 1905. In the case of narcissi and gladioli, interspecific hybridization was used extensively, and this led to the release of improved cultivars. The same was true for *Lilium* (Rockwell et al. 1961) and bulbous irises (Dix 1974a), which were actively hybridized after the beginning of the 20th century.

These hybridizations programs led to an increase in cultivar diversification and contributed significantly to the global development of the flower bulb industry. The selected characteristics of the cultivars were influenced directly by their projected uses and the economic/social situations. Also, the evolution of scientific knowledge established possibilities for technical advances. For example, in the 17th to 19th centuries, tulips were marketed as single bulbs (Doorenbos 1954). However, as the economies of the countries grew, bulbs were widely used in gardens in groups. Later, they were used as fresh-cut flowers and then potted plants (see Section IV). Although forcing of the tulip 'Duc van Tol' was reported in 1760 (Pavord 1999), commercial forcing increased significantly when Nicolaas Dames, a Dutch bulb grower, developed the basic techniques for hyacinths in 1910 (Doorenbos 1954). It is noteworthy that these basic techniques still are used today. Mass utilization of flower bulbs progressed as the primary focus changed from gardening to a commercial flower bulb and cut flower forcing industry (see Sections III and IV.C.3).

The Netherlands dominated the total world bulb trade during the 19th and 20th centuries; at the end of the 20th century, the country controlled about 92% of the trade (Anon, 1999). This situation is slowly changing, however, due to four factors: (1) bulb production areas are being displaced by housing developments as the population of the Netherlands increases; (2) the need for fresh soils; (3) the need to decrease production costs, and especially labor, for consolidation of bulb growers and exporters; and (4) the production of high-quality bulbs in other countries (Gould 1957; Kiplinger and Langhans 1967; Wallis and Mather 1977; Moore 1984; Schenk 1984; Smith and Danks 1985; Van Nes and Komijn 1988; Anon, 1992). Several histories on the development of the flower bulb industries have been published, including in the Pacific Northwest of the United States (Gould 1957, 1993), in the

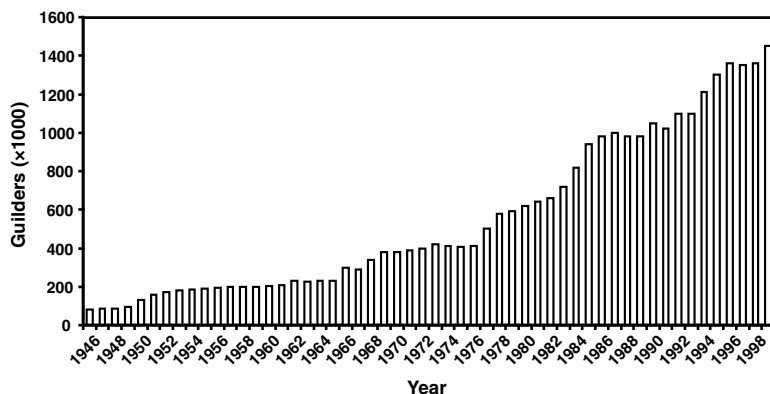


Fig. 1.1. Export value (guilders) of flower bulbs from the Netherlands from 1946 to 1999.

United Kingdom (Tompsett 2006), and in the Netherlands (Franken 1931; Krelage 1946).

III. GLOBALIZATION OF THE WORLD FLOWER BULB INDUSTRY

A. Utilization and Development of Expanded Markets

Worldwide, the value of the flower bulb industry is estimated to be over \$1 billion, and the most popular bulbs are tulip and lily (Fig. 1.1, Tables 1.2 to 1.5; De Hertogh and Le Nard 1993c; Buschman 2005). Import and use of flowers of ornamental bulbs occupy a noticeable place within global cut flower production. In 2005, 16 leading countries produced ornamental geophytes of 15 most popular genera on more than 32,000 ha (Table 1.2). In the Netherlands, the leading bulb producer worldwide, the production value in 2005 was US \$29,491/ha, while the export value was \$34,048/ha (AIPH 2006). The total flower bulb export of the Netherlands in 2005 was \$756 million, of which \$406 million for forcing and \$350 million for dry sale, while total export from the European Union (EU) countries was over \$837 million (Van der Veer 2006).

Seven of the most popular genera (*Crocus*, *Gladiolus*, *Hyacinthus*, *Iris*, *Lilium*, *Narcissus*, and *Tulipa*) represent about 90% of the production area devoted to geophytes (Table 1.2). Production of tulip bulbs takes place at least in 15 countries, with the largest production area being in the Netherlands with 10,800 ha (88% of global production). The Netherlands produces more than 4 billion tulip bulbs, of which 2.3 billion (53%) are used for cut flower production in different countries. Tulip bulbs are also produced in Japan (300 ha), France

Table 1.2. The estimated world production of ornamental geophytes (flower bulbs) in 2002/2003 (Buschman 2005).

Country	Hectares	Major flower bulbs produced
The Netherlands	20,921	Tulip, Lily, <i>Narcissus</i> , <i>Gladiolus</i> , Hyacinths, <i>Crocus</i> , <i>Iris</i>
UK	4,660	<i>Narcissus</i> , <i>Gladiolus</i> , Tulip
France	1,289	Lily, Tulip, <i>Iris</i> , <i>Gladiolus</i> , <i>Dahlia</i> , <i>Narcissus</i>
China	1,281	<i>Narcissus</i> , Lily, Tulip
USA	995	<i>Narcissus</i> , Tulip, <i>Gladiolus</i> , Lily, <i>Iris</i>
Japan	883	Lily, Tulip, <i>Gladiolus</i>
Israel	456	<i>Narcissus</i> , <i>Ranunculus</i>
Poland	335	Tulip, Lily, <i>Narcissus</i> , <i>Gladiolus</i> , <i>Dahlia</i>
New Zealand	258	Tulip, Lily, <i>Zantedeschia</i> , <i>Iris</i> , <i>Freesia</i>
Chile	240	Lily, Tulip
South Africa	200	<i>Hippeastrum</i> , <i>Nerine</i> , Lily, Tulip
Brazil	200	<i>Gladiolus</i> , <i>Hippeastrum</i>
Germany	190	Tulip, <i>Gladiolus</i> , <i>Narcissus</i> , <i>Crocus</i>
Belgium	185	<i>Begonia</i> , Lily
Denmark	60	Tulip, <i>Narcissus</i>
Argentina	47	<i>Gladiolus</i> , Tulip
Total	32,200	

(293 ha), Poland (200 ha), Germany (155 ha), and New Zealand (122 ha) (Buschman 2005).

The global production of lily bulbs occurs in 10 countries. The largest production area is also in the Netherlands 4,280 ha (77%), followed by France (401 ha), Chile (205 ha), the United States (200 ha), Japan (189 ha), and New Zealand (110 ha) (Buschman 2005). The Netherlands produces 2.21 billion lily bulbs, of which 2.11 billion are exported to the countries within the EU (1.0 billion) and outside the EU (0.7 billion). In the Netherlands, 0.41 billion lily bulbs are used as cut flowers.

Table 1.3. Production of Dutch-grown flower bulbs in 2003/2004, 2004/2005, and 2007/2008 (PT/BKD 2008).

Types	Hectares		
	2003–2004	2004–2005	2007–2008
Tulips	10,982	10,034	9,885
Lilies	3,212	3,275	3,699
Narcissi	1,796	1,721	1,687
Gladioli	1,151	1,060	1,019
Hyacinths	1,121	1,140	854
Crocuses	668	566	463
Irises	481	464	360
Total	19,411	18,260	17,967

Table 1.4. Sales of Dutch-grown tulip and lily bulbs (million) in 2002/2003 (after Buschman 2005).

Country/Region	Tulip bulbs		Lily bulbs	
	Total sales	Cut flowers	Total sales	Cut flowers
The Netherlands	1,320	1,300	410	410
EU	1,900	630	1,060	1,000
Outside the EU	1,100	370	740	700
USA	441	147	170	150
Japan	238	90	158	143
Canada	95	48	20	18
Norway	79	60	—	—
Poland	57	29	23	19
Mexico	—	—	50	50
Switzerland	36	12	—	—
Australia	30	15	43	41
Taiwan	—	—	38	38
Russia	30	8	25	25
China	28	14	60	75
Korea	12	11	24	24

Currently, the EU and the United States are the leading export markets for flower bulbs, but the ranking of the countries has changed significantly over time (Tables 1.4 and 1.5). It has been influenced by world wars, quarantines, and changing markets. Using the principles established by Blaauw and coworkers (Hartsema 1961), the Netherlands has focused primarily on the commercial forcing of tulips, Dutch irises, and daffodils as fresh-cut flowers. In contrast, in the United States, the primary use of forced flower bulbs has been as flowering potted

Table 1.5. Primary marketable products of ornamental geophytes produced in the Netherlands (Van der Veer 2006).

Country	Value in million US dollars			Ratio (landscaping: forcing)
	1996–1997	1999–2000	2005–2006	
USA	115	147	179	2:1
Japan	114	102	102	1:3
Germany	95	90	104	2:1
UK	51	65	97	3:1
Italy	53	61	56	1:4
France	55	56	65	2:1
Sweden	24	24	28	1:2
Canada	15	20	29	1:1

plants (De Hertogh 1996; USDA/NASS 2007). Two-thirds of the imported and domestically grown bulbs in the United States are used in gardens and landscapes. The United States has been an increasing market for the last three to four decades (Ogden 2007); however, in all markets, horticultural uses change slowly. The consumer has focused not only on longer-lasting and more reliable plants and flowers but also on an expanded variety of flower colors, plant types, and other horticultural characteristics. The tulips and lilies cultivated in the southern hemisphere (Table 1.2) are used for autumn flowering (October–December) in the northern hemisphere, especially in the United States, the Netherlands, Japan, Taiwan, China, and Canada.

Worldwide, the floricultural sector has, and will continue to, experience changes. In addition to traditional countries (Table 1.2), globalization and increased competition have led to the development of new bulb and flower production centers. For example, floricultural production in Latin America, Africa, and Asia is increasing rapidly. In addition, China, India, Malaysia, Pakistan, Taiwan, Thailand, Singapore, Sri Lanka, and Vietnam are emerging as flower producers.

It is anticipated that the north-south axis will be important to the export market. Africa will increase flower export to Europe and South America to the United States and Canada. Within Asia, there will be a growing interregional trade with emerging countries such as Malaysia, Thailand, and the Philippines. Australia and New Zealand have the potential to enter the niche market in Asia with high-quality bulb and flower products (De Groot 1999).

For many years, the cultivation of flower bulbs basically was restricted to countries with developed ornamental horticulture industries and moderate climates. Four centuries of bulb production, breeding, the development of new products, and an extensive bulb export trade led to the clear leadership of the Netherlands in this domain. In fact, most consumers of flower bulbs believe that all flower bulbs originate and are produced in the Netherlands. However, with the globalization of the horticultural trade, transfer of knowledge, and economic progress of the developing countries, bulb production is no longer limited to countries with a prevailing moderate climate. The production of bulbs and bulb flowers of high quality in various regions has become important during the last decades of the 20th century. This growth has been stimulated by relatively inexpensive land and labor costs and the expansion of international trade (Table 1.4). With the development of landscape architecture and increases in private gardening in warm-climate regions, bulbs have become popular not only in the southern parts of the United States and Europe but also in Asian countries and Australia.

B. Introduction of New Crops

Bryan (1989, 1994, 1995, 2002) has reported four highly defined centers of origins that account for many species:

1. The perimeter of the Mediterranean region (Greece, Italy, Northern Africa, Spain, Turkey)
2. Asia (China, Japan, Russia)
3. The mountain regions extending from Chile in South America to the state of Washington in the United States and the province of British Columbia in Canada
4. Southern Africa, in which the largest total number of genera has been found.

High diversity of native geophytes can be also found in the Irano-Turanian floristic region (Iran, Afghanistan, Central Asia), and in subtropical zones (Fig. 1.2).

Currently, research efforts are focused on the development of new commercial crops and suitable production procedures. The utilization of new ornamental geophytes could be greatly expanded by increased plant evaluation and increased collaboration among researchers, extension specialists, and growers. Obviously, questions of technology transfer, legal aspects, and sharing of benefits must be in accord with the Convention of Biological Diversity (UNEP 1992; www.biodiv.org/convention/articles.asp) and must be considered in relation to each case of new crop development (Coetzee 2002; Kamenetsky 2005).

Market saturation with traditional plants and flowers has stimulated an increased interest in novelties. Thus, many countries are evaluating their indigenous flora as a source of potential ornamental crops. A major reason for genetic resource conservation is to ensure that the diversity will be available for future breeding programs and sustainable production. It is also clear that the industry must be able to react rapidly and efficiently. Regions where intensive research on new crops is occurring include: Israel (Halevy 2000; Kamenetsky 2005); Australia (Plummer et al. 2000); South Africa; and northeast Asia, comprised of Japan, Korea, China and Taiwan (Ohkawa 2000). In addition, a special Ornamental Plant Germplasm Center was created in the United States in conjunction with the USDA National Plant Germplasm System and Ohio State University (Tay 2003). Concurrently, most countries lack of knowledge about indigenous plant genetic resources, a fact that hinders the development of new crops (FAO 1998).

The Middle East and Central Asia are the origins of almost all the currently grown “classic” bulbous crops, but other potentially useful

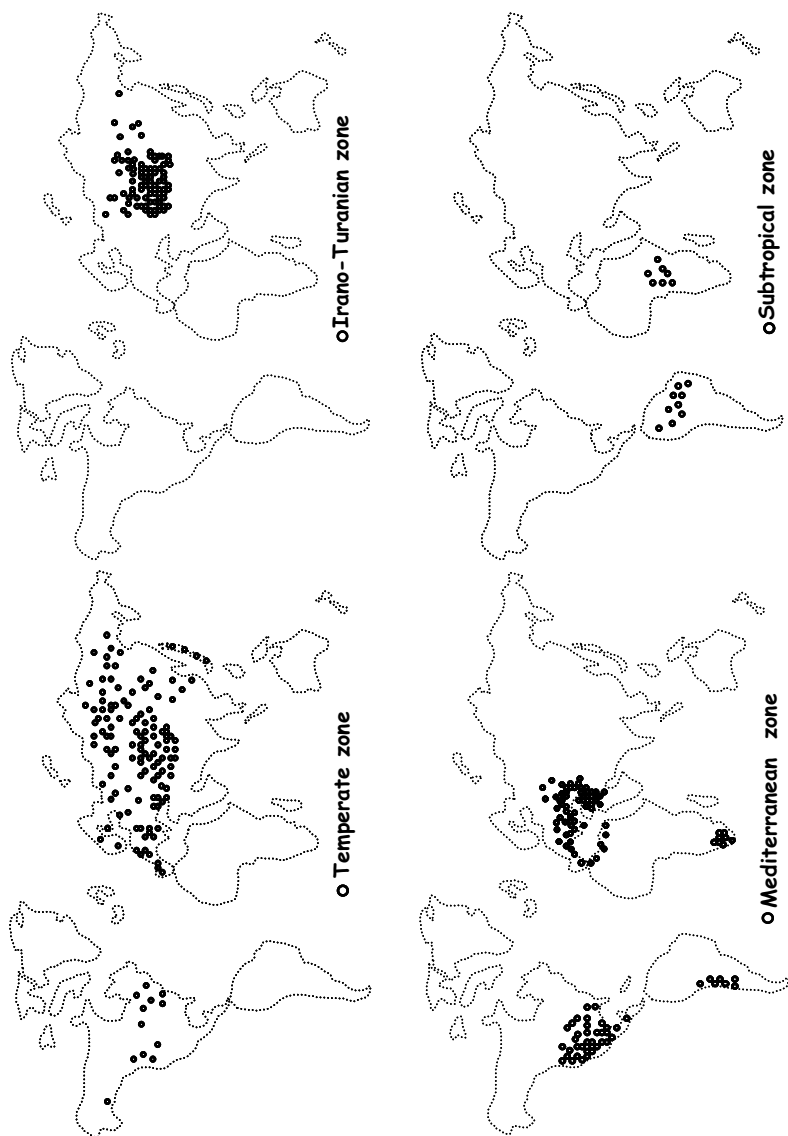


Fig. 1.2. World origins of ornamental geophytes (flower bulbs).

species can be found in these regions (Avishai et al. 2005). The wild *Allium* species have the potential to become new bulb crops that could increase the variety of cultivated flower bulbs (Kamenetsky and Fritsch 2002). A special collection of ornamental *Allium* species was established in Israel to be used for the evaluation and development of new ornamental crops (Kamenetsky 1993). In addition, Mediterranean species of *Scilla*, *Pancratium*, *Iris*, and *Fritillaria* have potential (Halevy 2000; Avishai et al. 2005; Kamenetsky 2005).

The flora of South Africa, which includes over 2,700 flower bulb species, has provided horticulture with the well-known *Gladiolus*, *Freesia*, *Nerine*, and *Zantedeschia* (calla lily), but other species need to be evaluated, bred, and developed. These species are known as specialty bulbs: *Ixia*, *Agapanthus*, *Gloriosa*, *Cyrtanthus*, *Lachenalia*, and *Babiana* (Du Plessis and Duncan 1989; Ehlers et al. 2002; Niederwieser et al. 2002).

South America also has a diverse bulbous flora and these resources have not been fully explored. A collection of ornamental *Alstroemeria* and *Hippeastrum* species native to Brazil was started in 1989 (Tombolato et al. 1992; Tombolato and Matthes 1998). It has a goal of creating types of plants and flowers that are uniquely different from existing commercial cultivars. Other genera—for example, *Griffinia* (Amaryllidaceae), *Neomarica* (Iridaceae), and *Gomphrena* (Amaranthaceae)—have been collected because of either their showy flowers or unique growth habit (Tombolato and Matthes 1998). New cultivars of *Eucrosia* (Roh et al. 1992; Meerow et al. 1992b) have been developed and are being produced commercially.

Research projects on the breeding, propagation, physiology, and production of flowering geophytes from Chile have been in progress for several years (Bridgen et al. 2002). Various interspecific and intraspecific hybrids of *Alstroemeria* species have been bred by means of a combination of traditional and biotechnological techniques. Other species that are being bred and studied include: *Conanthera bifolia*, *C. campanulata*, *C. trimaculata*, several *Rhodophiala* spp., *Zephyra elegans*, *Leontochir ovallei*, *Pasithea caerulea*, and *Herbertia lahue*. Genotypic differences have been evaluated for the unique Chilean species *Leucocoryne coquimbensis*, *L. coquimbensis alba*, *L. purpurea*, and *L. ixioides*. All these have potential for increased breeding and development (Bridgen et al. 2002). The Australian native plant *Anigozanthos* (Haemodoraceae), which is known as the kangaroo paw was grown mainly outdoors until a few years ago (Goodwin 1993). However, recently introduced high-yielding interspecific hybrids are being greenhouse-grown for year-round production as potted plants. These new hybrids are

propagated by in vitro tissue culture (Halevy 1999). In Japan, the endangered species *Arisaema sikokianum*, which is endemic to the Shikoku and Honshu islands, has been evaluated for commercial use (Fukai et al. 2002).

C. International Conventions

To date, seven Conventions on Biodiversity (CBD) have been ratified. The next one will be in 2010 (www.biodiv.org). This movement started in 1992 in Rio de Janeiro in the United Nations Conference on Environment and Development (UNCED). At this time, it was decided that countries have sovereign rights over their biological sources. A global overview approach to the problems of conservation and sustainable use of the world's biodiversity brought the utilization of genetic resources to an important point. Thus, the CBD evaluate the development of the horticultural trade, including the diversity of ornamental geophytes. This is important since some of these species are approaching extinction and the goal is to protect them.

The Convention of International Trade of Endangered Species of wild fauna and flora (CITES, www.cites.org) was established in 1973. The aim of CITES is to regulate and monitor the international trade of selected species of plants and animals to ensure that trade does not endanger the revival of the wild population. There are three taxa of flower bulbs on the CITES list: *Galanthus*, *Cyclamen* (all species except *C. persicum*), and *Sternbergia* (Davis et al. 1999; McGough et al. 2004). For *Galanthus*, the primary center of origin is Turkey. In spite of the fact that *Galanthus* bulbs are an important income for the local villagers, a comprehensive control system to monitor and regulate the collection and trade is needed. Thus, for export of the bulbs, these crops require a special permit that is issued by the CITES office of that country.

IV. MAJOR AREAS OF RESEARCH

This and the next part highlight the findings of groups and individuals who have contributed significantly to the globalization of the flower bulb industry.

The research of Professor Anton Blaauw and his coworkers from the 1920s to the 1950s in the Netherlands (Hartsema 1954, 1961) provided the scientific physiological foundation for the bulb industry, both nationally and internationally. Bulb morphology, the physiology of flower initiation and development, and the temperature treatments required for early forcing and retarded flowering were their primary research

areas. This research has contributed not only to the knowledge of the crop biology but also practical aspects of bulb and flower production (Blaauw 1923a). Hartsema (1954, 1961) has summarized most significant achievements of this group:

1. Early production of fresh-cut flowers of tulips, hyacinths, daffodils, bulbous irises, and freesias that was based on the control of flower formation and rapid stem (scape) elongation primarily by temperature.
2. The retardation of flowering for export to the southern hemisphere by the use of low (e.g., tulip and hyacinths) or high temperatures (e.g., hyacinths, daffodils, irises).
3. The release of bulb dormancy by applying low (e.g., in *Convallaria*) or high (e.g., in freesias) temperatures.
4. The prevention of flowering in small bulbs (e.g., Dutch irises) by using low temperatures.

This research was complemented by the allied programs conducted at the LBO (PPO) in Lisse, the Netherlands (see Section V.B.1).

Outside of the Netherlands, research was generally focused on resolving the requirements for bulb growth and flowering of other flower bulb crops. For the major commercial species, research was focused on adapting or improving the Dutch techniques used for bulb and flower production and marketing. This was necessary due to specific climatic and agronomic conditions and, sometimes, the specific market requirements. Some examples are: (1) Easter lilies and potted tulips in the United States; (2) the use of “French Tulips” for early and long-stemmed cut-flower forcing; (3) winter production of cut flowers in Israel, and (4) flower production in southern hemisphere. This research was supplemented by basic research on the physiological processes of bulb and flower growth and development. The effects of environmental factors and plant growth regulators (PGRs) (see Section IV.D.5) were also studied. In addition to these physiological approaches, breeding was conducted in the United States, Japan, France, and Israel in order to obtain cultivars that are highly adapted to local conditions. Research on in vitro culture for rapid propagation of healthy plant material and new cultivars has been conducted in Israel, Japan, Great Britain, France, and the United States.

Other research has focused on the introduction of new species and their adaptation to specific market requirements. Some examples are:

- In Israel, *Ornithogalum dubium*, *Leucojum aestivum*, and *Paeonia*
- In New Zealand, *Zantedeschia* and *Sandersonia*

- In South Africa, *Ixia*, *Agapanthus*, *Gloriosa*, *Cyrtanthus*, *Lachenalia*, and *Babiana*
- In Chile, *Alstroemeria* and *Leucocoryne*

These programs generally combined physiology, breeding, and in vitro culture.

Research on disease and pest control (see Section IV.D) has been important not only for the countries with developed bulb production (e.g., the Netherlands and U.K.) but also for countries importing bulbs. Quarantine regulations (e.g., in the United States and Japan) have stimulated domestic bulb production (Gould 1993). Due to many differences in national pesticide regulations, research and experiments concerning the chemicals used for disease and pest control were carried out in most countries that either produce and/or import flower bulbs.

A. Plant Breeding and Genetics

Like other ornamental plants, plant breeding, spontaneous mutations, and changes in ploidy levels in flower bulbs (Doorenbos 1954) have been important in cultivar diversification. They have contributed significantly to the development and diversity of the flower bulb industry.

During the past 60 to 70 years, the major breeding objectives have been the improvement of traits of importance for horticulturists (e.g., plants with short forcing periods and the ability to grow using high planting densities and low light conditions). The commercial cultivars for cut flower production must satisfy the major requirements of the bulb growers: excellent bulb enlargement and propagation rates, disease resistance, and adaptation to mechanical operations during planting, harvesting, and grading (Fig. 1.3). Vase life is a very important trait for the consumer; however, it has not always been considered by plant breeders. The research devoted to these various factors will be reviewed in this part.

The role of plant breeding and genetics varies according to the genera and is affected by several factors (Le Nard and De Hertogh 1993b, Le Nard 2000). Five major factors are described next.

1. The existence of genetic variability and the possibilities of using that variability. In *Gladiolus*, *Lilium*, and *Narcissus*, interspecific hybridizations can be used for cultivar diversification. In contrast, in *Tulipa*, the possibility of interspecific hybridization is limited (Van Raamsdonk et al. 1995). *Hyacinthus* is an exception, because all forms have been derived from one species with limited variability,

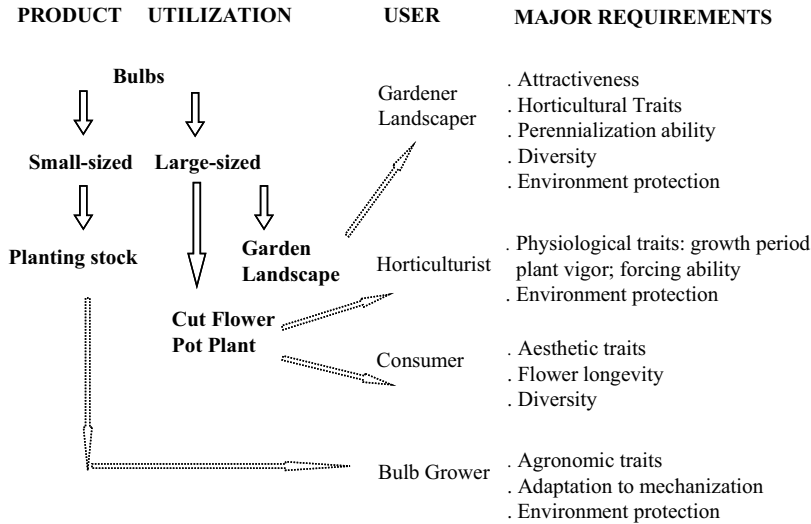


Fig. 1.3. Production and utilization of ornamental geophytes (flower bulbs).

but some cytological distinctive features (e.g., various levels of ploidy, including heteroploids) have produced a large cultivar diversification (Doorenbos 1954).

2. The rate of progress in plant breeding of flower bulbs is affected by the length of the juvenile phase (Le Nard and De Hertogh 1993b). The various genera and species demonstrate a great diversity for this characteristic. It can range from a few months for *Anemone* and *Ranunculus* and up to 5 to 6 years in tulips. When the first flowers of the crossings are produced, selections usually are restricted to only a few traits (e.g., flower color and shape). Additional growth cycles (clonal propagation) are required for a complete evaluation of other important traits.
3. The propagation rate is also an important biological factor that affects breeding efficiency. It determines the length of the phase between hybridization and the release of new cultivars to the industry. For those genera/species that are propagated by seeds, this phase can be short. For vegetatively propagated taxa, a large diversity exists not only in their natural propagation rates but also in their responses to artificial propagation techniques. Since the natural propagation rate of tulips is only 2 to 3 per year, and the use of artificial propagation techniques is limited, it takes about 25

years between the initial hybridization and the release of a new cultivar to the industry. In contrast, lilies can flower in the first year after the crossing, and they can be propagated easily by in vitro culture. Thus, a new cultivar can be introduced in a few years.

4. The possibility of genetic studies is significantly affected by the strong heterozygosity of most of the bulbous species.
5. In flower bulbs, the use of molecular techniques has many limitations due to the size of the genomes of the main genera. For example, the DNA content of unreplicated haploid genome of *Tulipa* spp. is about 200 times higher than the DNA content of *Arabidopsis thaliana*, the plant commonly used as model plant for molecular studies (Arumuganathan and Earle 1991).

When considering the economic factors affecting plant breeding, one has to consider that only a few genera are grown on a large commercial scale and their production encompasses a limited number of countries (Tables 1.2 and 1.3). Thus, only genera of economic importance are subjected to costly breeding techniques (e.g., biotechnology and genomic studies). These approaches can be carried only by specialized companies and by economically developed countries. As a consequence, the existence of breeding programs is generally linked to the social-economic situation of the countries and not necessarily determined by the wealth of the indigenous flora and/or by the potential of flower bulb production. Consequently, flower bulb breeding and cultivar diversification have been achieved largely by bulb growers and enthusiasts. However, in the past few decades, breeding has been performed by specialized companies and research institutes. The role played by bulb enthusiasts must not be overlooked, because they are of importance for many specialty bulbs, daffodils, and dahlias.

The breeding techniques used vary greatly according to the genera and their biological characteristics (e.g., existence/absence of sterility; the possibility of interspecific hybridization, and the possibility of using in vitro techniques). In some genera, such as tulips and hyacinths, spontaneous mutations play an important role in cultivar diversification (Doorenbos 1954). For example, among the 1,500 new tulip cultivars registered from 1996 to 2005, about 28% of them are mutants, and most have been spontaneous mutants (Bodegom and Van Scheepen 2005).

An effective breeding program must include efficient screening techniques for important physiological and agronomic traits. It is known that the growth of ornamental geophytes is affected not only by the growing conditions but also by the conditions under which the mother

bulbs were previously produced and stored. In addition, a strong genotype $\times$ environment interactions exists in flower bulbs. Thus, knowledge of the physiology of the genera or species being bred is necessary in order to determine the screening techniques to be used and the horticultural characteristics to be recorded.

1. Breeders' Right and Variety Registration

Union of Protection of New Varieties [Cultivars] of Plants (UPOV, www.upov.int). Breeders' Right is registered in the different countries and can be obtained for one or more countries. In general, the breeder must supply a certain number of bulbs to the registration office for trials. Subsequently, an independent judging committee records not only the characteristics of the aerial organs of the bulb (e.g., flower color, uniformity, etc.) but also disease resistance. All registrations for the Breeders' Right Register must be paid annually by the applicant. Depending on the bulb group, the Breeders' Right is valid for 25 years, but the applicant can cancel the Breeders' Right at any time.

Community Plant Variety Office (CPVO). In Europe, the breeder can choose between the local Breeders' Right Office and the European office (CPVO) for the EU. If granted, a Breeders' Right issued by the local office is valid only for that country. If applied to the CPVO office, the Breeders' Right is valid for all EU countries. That means that the breeder has to apply to the local office in countries such as Japan and the United States to obtain Breeders' Right for the cultivar in those countries. If granted, an annual fee must be paid to CPVO for maintaining the Breeders' Right. More information on the crops and cultivar names that have been registered since 1995 or are still active under procedure can be found on www.cpvo.eu.int.

Registration. The two official registration offices for flower bulbs are the Royal Horticultural Society (RHS) for daffodils (Kington 1998) and lilies (Leslie 1982; Matthews 2007) and the Royal General Bulbgrowers' Association (KAVB) for tulips (Van Scheepen 1996; Bodegom and Van Scheepen 2005) and hyacinths and specialty (formerly called miscellaneous) bulbs (Van Scheepen 1991). These registration organizations were appointed by the International Society for Horticultural Science (ISHS). The nomenclatural bodies are a division of the UNESCO (Trehane 1995). To register a name, they must follow the rules of the International Code of Nomenclature for Cultivated Plants (1995). The registrant does not have to pay a fee for the registration.

2. Hortus Bulborum: A Germplasm Repository. A collection of approximately 1,500 tulips, 800 daffodils, 80 hyacinths, 22 irises, 49 crocuses, and 17 *Fritillaria* cultivars and species are maintained in this collection located at Limmen, the Netherlands (Leijenhorst 2004). This collection was initially maintained and registered by Mr. P. Boschman, a horticulture teacher and head of a primary school. The collection of old hyacinth cultivars was a part of the research program of Dr. W. E. de Mol in Amsterdam. Since 1908, his research focused on variability in flower bulbs; after 1915, it included breeding and cytology of bulbs and especially hyacinths. In 1928, the two collections were merged under the name "Hortus Bulborum." The collection is cultivated on the fields of the flower bulb company Van't Hof and Blokker. Initially the collection was private, but in 1934 the NEVERSIE (Nederlandse vereniging tot bevordering der wetenschappelijke VERedeling van SIErgewassen) Society was established and became the owner/advisor of Hortus Bulborum. The goal of the society was to improve the quality of horticultural products, especially bulbous crops, by using old cultivars for breeding purposes. They selected for characteristics such as earliness and disease resistance. The oldest tulip cultivars in the collection are 'Duc van Tol Red and Yellow' (1595) and 'Zomerschoon' (1620). The 'Double Campernelle' (pre-1611) is the oldest daffodil cultivar, and 'King of the Blues' (1863) is the oldest hyacinth cultivar. In 1963, the IVT (currently the PRI) became involved. The first project was to determine the number of chromosomes of the different cultivars/species (Zeilinga and Schouten 1968). This was followed by several breeding projects: for example, for *Fusarium* and TMV (tobacco mosaic virus) resistance, earliness, and keeping quality (Van Eijk and Varenkamp 1979; Van Eijk et al. 1986a). However, any flower bulb breeder can use the collection to obtain pollen (pollen bank) for their program. In 1991, the Hortus Bulborum became an independent foundation (Stichting) in order to maintain and expand the historical collection.

3. Gladiolus. The genus includes more than 150 species that are mainly native to eastern, southern, and western regions of Africa, but about 12 species originate in the Mediterranean region (Cohat 1993). The first species were introduced to Europe prior to 1740 (Beal 1927). The modern cultivars were developed by interspecific crosses that started as early as 1807 and continued during the 19th century in Great Britain, France, Germany, the Netherlands, Belgium, and the United States (Fairchild 1953; Ohri and Khoshoo 1985). Only 8 species, all of them originating from Africa, were used in these interspecific crosses. They led to the creation of two types of hybrids: spring flowering and summer

flowering. The spring-flowering types were the results of intercrosses between diploid species, and they were widely cultivated in Europe by the middle of the 19th century. After 1839, their popularity waned because of the successful hybridization between a diploid and a hexaploid species that produced tetraploid plants. These summer-flowering hybrids had vigorous growth characteristics, long and strong floral spikes, and were adapted to the European climatic conditions. These hybrids were a significant turning point in the evolution of the garden gladioli. They provided the genotypes for the summer-flowering cultivars that currently are used worldwide not only in gardens but also for commercial cut-flower production.

Repeated intercrossing between the tetraploid summer-flowering hybrids, plus interspecific crosses with three additional polyploid species, produced the diversified group of large-flower-size cultivars (Fairchild 1953; Ohri and Khoshoo 1985). Most of these cultivars were bred and released by professionals and amateurs in various parts of the world, such as the United States, Canada, Europe, Australia, and New Zealand. In each country, the selection criteria varied. For example, ruffled or laciniated flowers were mainly selected in the United States and Canada (Fairchild 1953). In Europe, and especially in the Netherlands in the last few decades, special attention was given to the breeding of cultivars adaptable to cut-flower production.

It must be noted, however, that for the past 20 years, the importance of gladioli has been decreasing worldwide (Anon, 2000). In the Netherlands, corm production has steadily decreased from 2,145 ha in 1991 to 1,019 ha in 2007 (De Hertogh and Le Nard 1993c; PT/BKD 2007). Although 125 cultivars of the summer-flowering types were grown, only two of them occupied more than 50 ha, while the 12 spring-flowering cultivars were grown on only 19 ha (PT/BKD 2007, www.bloembollenkeuringsdienst.nl).

Due to their complex interspecific origin, the modern large-flowered cultivars are tetraploid and heterozygous, which makes genetic studies very complicated. Cohat (1988) showed that the heritability of quantitative characteristics such as earliness of flowering, plant height, spike length, and the number of flowers per spike was medium to high. Conversely, qualitative traits, such as inflorescence esthetic value and the general attractiveness of the plant, have a very low heritability. Thus, excellent parents can produce poor progenies, and the phenotypic value of parents does not permit a prediction of the horticultural characteristics of the offspring.

Breeding for disease resistance is also a major challenge. *Fusarium* is a major soil-borne disease that can be a serious problem for corm

production, especially under warm climates. The evaluation of numerous cultivars and species by the U.S. Department of Agriculture (USDA) (Palmer and Pryor 1958; Palmer et al. 1965), and in the Netherlands (Löffler et al. 1997; Roebroek and Mes 1992; Straathof et al. 1998) indicated the existence of sources of resistance in some species and in the large-flowered group. The breeding program in Florida (Wilfret and Magie 1979; Wilfret 1981, 1986) has produced some positive results. However, the existence of physiological races of *Fusarium* could make it difficult to obtain total resistance. To accelerate the selection process for resistance to *Fusarium*, Straathof et al. (1997) studied a technique using seedling populations. Also, the possibility of an in vitro selection for *Fusarium* resistance, using cell suspension cultures and challenged by fusaric acid, was studied by Remotti et al. (1997), but no practical applications have been reported.

Dry rot (*Stromatinia gladioli*) is another serious disease during corm production, especially in the Netherlands. A testing method for selecting resistant material was evaluated by Van Eijk et al. (1990). They found a degree of resistance in species native to the Mediterranean region, but these species could not be crossed with either the African species or the commercial cultivars.

In South Africa, Ferreira et al. (1990) studied the resistance of commercial cultivars and species to gladiolus rust (*Uromyces transversalis*). They found no resistance in the commercial cultivars (none of them was bred in South Africa), but the response of the species varied from resistant to very susceptible. An important finding was that different ecotypes of the same species could express different responses to the contamination. Breeding for rust resistance has also been investigated in Brazil (Tombolato et al. 2002). The USDA/APHIS in the United States prohibits the import of corms or flowers with this disease. Thus, it has a worldwide impact.

In order to produce high-quality cut flowers during winter in the Mediterranean production areas, breeding programs for the selection of cultivars suitable for low-light conditions were established in France and Israel. South African diploid species that flower in the autumn or winter were crossed with tetraploid large-flowered cultivars (Poisson 1980). The hybridizations produced lines that combined a winter-flowering capability with an acceptable commercial value. The most attractive lines were marketed in the 1990s under the names of "Gladiolines" in France and "Orchidioli" in Israel. Their utilization, however, has been very limited due to the difficulties in corm production (*Fusarium* susceptibility) and the fact that the cut flowers were not widely accepted commercially.

Research on in vitro propagation techniques has produced many positive results (Ziv et al. 1970; Simonsen and Hildebrandt 1971; Hussey 1977; Bajaj et al. 1983; Ziv 1989; Steinitz and Lilien-Kipnis 1989; Kamo et al. 1990; Stefaniak 1994; Kasumi et al. 1998, 1999a,b). Successful genetic transformations for Gladioli has been reported by Kamo (1997) and Löffler and Van Harmelen (1998), but no commercial use of these results has been reported. The possibility of in vitro production of polyploid plants by using colchicine has been reported by Meyers (1996). Last, mutation breeding has been carried out, and some color mutants have been obtained (Moës 1966; Cohat 1980, pers. comm.). However, after corm or cormel irradiation, the selection of acceptable mutants can take several years. Thus far, none has been released.

4. Hyacinthus. Hyacinths differ from most economically important flower bulbs because all the commercial cultivars belong to one species, *Hyacinthus orientalis*. The species is indigenous to Asia Minor and was first described in 1562 by de L'Obel (Dix 1974b). In 1581, he also described another flowering type called "Roman Hyacinths": *H. orientalis* var. *albulus* (Dix 1974b). At that time, blue-, white-, and purple-flowering cultivars had been identified. Double-flowering types were described in 1612, and they remained popular until the middle of the 19th century (Doorenbos 1954).

Breeding was started in the Netherlands at the beginning of the 18th century and was conducted primarily by wealthy amateur breeders. Pink- and reddish flowering types were obtained about 1709 and yellow-flowering types in 1760 (Doorenbos 1954). Subsequently, breeders produced numerous cultivars. At their peak of production, over 2,000 cultivars were grown. Some are in Hortus Bulborum (see Section IV.B.3). Even though the number of cultivars decreased after the second half of the 19th century, breeding continued in the Netherlands. Some cultivars—for example, 'L'Innocence' (1863), 'City of Haarlem' (1893), and 'Pink Pearl' (1922)—are still produced commercially in the Netherlands (PT/BKD 2007).

After 1910, when Nicolaas Dames demonstrated that Dutch-grown bulbs could be forced in December, the breeding objectives and uses of hyacinths changed significantly. The focus became forcing. In spite of the fact that only one species is available for breeding, new types are still being bred and released. This can be due to the fact that cytological studies revealed some peculiarities of hyacinths, and a number of them are heteroploids (Doorenbos 1954). By using the "Roman Hyacinth Types," cultivars producing several flowering stems per bulb have been obtained (Dix 1974b).

Hyacinth breeding has, and currently is, carried out largely by private companies. The exceptions are cytological studies (De Mol 1935; Hosokawa 1999) and resistance to yellow disease (*Xanthomonas hyacinthi*) (Van Tuyl and Toxopeus 1980; Van Tuyl 1982). Flower color, especially yellow, is an important goal of hyacinth breeding. Yellow cultivars tend to have a low vigor and are susceptible to diseases but do have a reasonable bulb production (Krelage 1883).

The physiological disorder called floral stalk topple (Shoub and De Hertogh 1975) is well known in hyacinths, but until recently it has had a low priority in the breeding programs. At the HOBAGO Testcentrum in Hillegom, the Netherlands, breeding has focused on having a strong floral stalk combined with an inflorescence with many florets. In 2007, three cultivars (Baltic Sea, Deep Sea, and Woodbells) were registered by the Testcentrum at the KAVB.

5. *Iris* (Bulbous). The genus *Iris* is diverse and includes many rhizomatous and bulbous irises (De Munk and Schipper 1993). Economically, the bulbous Irises are the most important, and they are divided into three major groups: “Reticulata,” “Juno,” and “Xiphium” (De Munk and Schipper 1993). The latter group is the most important for flower bulb industry. Most of the commercial cultivars belong to the Dutch *Iris* (*Iris* × *hollandica*) group, which was derived from crosses between *Xiphium* species and specific cultivars. Two *Xiphium* species were important in the development of the commercial cultivars: *X. vulgare*, native to the Iberian peninsula, and *X. tingitanum*, which is native to Morocco. These species differ in chromosome numbers and vigor. The *X. vulgare* types have a wide range of flower colors (white, blue, yellow, bronze); the *X. tingitanum* types have only blue and white flower colors. The *X. vulgare* types are small bulbous cultivars and can flower with a bulb that is 5 cm to 6 cm in circumference; the *X. tingitanum* are large bulbous types and flower only with bulbs greater than 8 cm in circumference. However, the *X. tingitanum* types have more potential for early and retarded (year-round) flowering. Currently, the large-bulbing cultivars represent about 90% of the total acreage devoted to *Iris* bulb production in the Netherlands (PT/BKD 2007).

Iris breeding started at the beginning of the 20th century in the Netherlands (Dix 1974a), and initially the “Spanish” irises (*X. vulgare* group) and numerous cultivars were released. There were, however, two very important breakthroughs: the successful interspecific crosses between small-bulbing cultivars of the *X. vulgare* group and the crosses between the two different types of the *X. tingitanum* species. Subsequently, these crosses produced large-bulbing cultivars—for

example, 'Wedgwood', 'Prof. Blaauw', and 'Blue Magic'—and they are adapted to year-round flower production (Dix 1974a). 'Blue Magic' is still the most widely grown cultivar in the Netherlands. In the season 2006–2007, 109 ha out of the 379 ha devoted to bulbous *Iris* were planted with 'Blue Magic' (PT/BKD 2007).

Initially, breeding with these interspecific hybrids was limited since they were sterile. However, a fertile spontaneous tetraploid of 'Wedgwood' was observed about 1952 (Eikelboom and Van Eijk 1990). Thus, it was possible to make crosses with cultivars of the *X. vulgare* types, and several triploid cultivars were produced. Among them was 'Telstar'. Currently, this is the second most important cultivar in the Netherlands and was grown on 52 ha in the 2006–2007 season (PT/BKD 2007). Under the very different growing conditions in western France (Brittany), a few fertile plants were found in 'Prof. Blaauw' in 1974 (Le Nard, unpublished data). The seeds were collected, and they produced fertile plants that appeared to be tetraploids. These plants were intercrossed and also crossed with diploid cultivars. The resulting selections were released to the growers in the 1990s.

Scientific research devoted to *Iris* breeding has been limited, and most of the plant breeding has been carried out by *Iris* growers. One program was developed in the Netherlands with the goal of using interspecific hybridization in order to obtain cultivars in various colors that could be flowered year-round (Eikelboom and Van Eijk 1990). The research provided some data on the transmission of flower colors, but the production of fertile tetraploid plants through the application of colchicine to scales was not successful. Perhaps the combination of mitotic substances and in vitro culture can be used for the bulbous *Iris* (Kim and De Hertogh 1997).

At present, the breeding and development of cultivars of *Iris* is carried out only by bulb companies. This situation probably is related to the fact that during the last two decades of the 20th century, interest in bulbous *Iris* has decreased in the Netherlands. For example, while 924 ha were devoted to *Iris* bulb production in the 1987–1988 season (PVS/BKD 1988), only 360 ha were grown in 2007–2008 season (PT/BKD 2008).

6. *Lilium*. The genus includes about 100 species that are native to North America, Europe, and Asia (Beattie and White 1993). There is a large diversity in plant architecture, flower shapes, colors, sizes and fragrance, and bulb morphology within these species. The cultivars that are currently popular are derived primarily from species originating from Japan and China. *L. × elegans* is considered to be a natural hybrid of *L. maculatum* and *L. dauricum*, and about 150 cultivars of *L. × elegans*

were developed and cultured by hobbyists in Japan in the mid-17th century during the Yedo period (1600–1867). Although they were not commercially used at the time, *L. longiflorum*, which is native to Ryukyu Archipelago, Japan, was described in 1784 by C. P. Thunberg using a dried specimen. Initially, live bulbs were introduced to the Royal Horticultural Society in the United Kingdom in 1819 via China and, subsequently, in 1830 to the Netherlands from Japan by P. F. von Siebold. Later this species, known today as Easter lily, replaced the Madonna lily in European countries where the majority of the population is Christian due to its vigor and the ability to control flowering by temperature (Kiplinger and Langhans 1967; Miller 1993). Many other *Lilium* species were also introduced from Japan in late 1800s, and they contributed to the establishment of lily breeding programs in European countries.

Lily breeding was initiated in Europe in the middle of the 19th century and increased dramatically after the beginning of the 20th century (Rockwell et al. 1961; Baardse 1977). Interspecific crosses played a fundamental role in the diversification of the cultivars. The major breeding research took place in Europe and the United States. A milestone for lily bulb and flower production was the breeding program that was initiated about 1940 by Jan de Graaff and his collaborators at the Oregon Bulb Farms (USA) with the assistance of some Universities (Rockwell et al. 1961; Baardse 1977). The first hybrid group released from this program was the Mid-Century Hybrids (now called Asiatic Hybrids). These hybrids have a complicated parentage that included *L. bulbiferum*, *L. dauricum*, *L. concolor*, and *L. tigrinum*, which are native to middle and far Asia (Rockwell et al. 1961). When introduced into the Netherlands about 1960, they were rapidly accepted. They adapted readily to the Dutch climatic conditions and, in addition, could be used for cut-flower production in greenhouses (Baardse 1977). Thus, lily usage changed from the garden to greenhouse forcing. The U.S. cultivars provided material for additional breeding programs that became established in the Netherlands. Even though their overall importance has decreased, bulb production of the Asiatic Hybrids still occupied 649 ha in the Netherlands in 2007 (PT/BKD 2007).

The second significant step was the production of the “Oriental Hybrid” lily group. It is composed of a very large group of hybrids using *L. auratum*, *L. speciosum*, *L. japonicum*, and *L. rubellum*, all of which are native to Japan (Rockwell et al. 1961). Initially, the breeding was carried out in the United States at the Oregon Bulb Farms; the USDA Laboratory in Beltsville, MD; and Boyce Thompson Institute in Yonkers, NY (currently at Ithaca, NY); and in Australia. The success of the “Oriental Hybrids” was due not only to their aesthetic value but also to the fact

that they could be used for cut-flower production. After their introduction in the Netherlands in the 1970s, their production rapidly increased, and new cultivars were bred and released. In 2007, 1,685 ha were devoted to bulb production of the Oriental Hybrids, which currently are the most cultivated group (PT/BKD 2007). Besides cultivars adapted to cut-flower production, some short-stemmed types that are adapted to potted plant production were also bred. This breeding program was initiated using a mutant selected in New Zealand (Baardse 1977).

Asiatic and Oriental hybrids have revolutionized lily bulb production and utilization and constitute the major part of the current lily bulb and flower production in the world (Rockwell et al. 1961). The exception is the Easter lily in the United States, which uses cultivars of *L. longiflorum* (native to Japan), but only for pot plant production for Easter. This production remains economically important in North America (Miller 1993). In the Netherlands, Israel, Japan, Korea, and China, bulbs of *L. longiflorum* are also produced in significant quantities, but the grown cultivars are used primarily for cut-flower production.

The introduction of the Asiatic and Oriental hybrids resulted in tremendous changes in lilies production. The Netherlands rapidly became the world leader in lily bulb and flower production, and active breeding programs were initiated after the 1970s. One major research effort was devoted to interspecific hybridization in order to improve the cultivars for characteristics such as virus, *Fusarium*, and *Botrytis* resistance; tolerance to low temperatures and low-light conditions; year-round forcing capabilities; and vigorous growth (Van Tuyl et al. 1986).

A major problem in lily breeding has been the failure to produce either intra- or interspecific crosses. Self-incompatibility studies were conducted with *L. longiflorum* by Brierley et al. (1937). Some of the successful procedures to overcome self-incompatibility include: the use of plant growth regulators (Emsweller and Stuart 1948; Emsweller et al. 1960), style heat treatments (Hopper et al. 1967; Hiratsuka et al. 1989), and the use of irradiated “mentor” pollen (Van Tuyl et al. 1982). Another solution was the breeding of *L. longiflorum* at the tetraploid level (Emsweller and Uhring 1960). A recent survey of natural populations of *L. longiflorum* in Ryukyu Archipelago of Japan and Taiwan has revealed that in the both north and south perimeter populations, self-compatible individuals are dominant (Sakazono et al. 2006).

Interspecific hybridizations have sexual barriers than can be classified into two groups: (1) prefertilization barriers and (2) postfertilization barriers. Research on these problems has been carried out in the Netherlands and Japan. In order to overcome incongruity

(a prefertilization barrier), two major techniques have been developed. The first technique is named cut style or amputated style (Myodo 1963; Van Tuyl et al. 1982, 1988), and the second is grafted style (Van Tuyl et al. 1991). Even though these two techniques can produce positive results, they are generally combined with various in vitro techniques in order to overcome the postfertilization barriers. Initially, embryo culture was used (North and Wills 1969; North 1975; Asano 1978). Later other techniques such as embryo rescue, ovary slice, ovary, and ovule culture were used successfully (Asano 1982; Van Tuyl et al. 1986, 1988, 1990b; Kanoh et al. 1988; Okazaki et al. 1995). This research has been summarized by Van Tuyl (1997) and has led to the production of many new interspecific hybrids, some of which are grown commercially in the Netherlands. This is especially true for *longiflorum* $\times$ Asiatic hybrids (L-A group), *longiflorum* $\times$ Oriental hybrids (L-O group), and Oriental $\times$ Trumpet Hybrids (O-T group). Bulb production for these latter hybrid groups occupied about 967 ha, 37 ha, and 236 ha, in the Netherlands in 2007 (PT/BKD 2007).

After the production of the interspecific hybrids, a subsequent problem is that these hybrids are often sterile. In order to overcome this sterility, breeding at polyploid levels has been studied (Van Tuyl et al. 1990a; Van Tuyl 1997; Van Tuyl and Lim 2003; Beers et al. 2005; Rhee et al. 2005). Polyploidy can be obtained by treating various tissues with colchicine, oryzalin, or dinitrogen oxide ("laughing gas"). The use of unreduced gametes also appears to be a promising technique for the introgression of desirable characters, such as disease resistance (Van Tuyl and Lim 2003; Beers et al. 2005). The use of molecular markers, which is currently not very adaptable in lilies, could be another interesting tool in breeding lilies for disease resistance (Krens et al. 2004).

In order to intercross genotypes exhibiting different flowering periods, pollen storage is necessary. This problem was investigated by Pfeiffer (1938), who demonstrated that pollen of *L. auratum*, *L. longiflorum*, *L. philippinense*, and *L. speciosum* could be stored up to 9 months by placing it at 10°C in humidity of 35%, 50%, and 65%. Recently, by using temperatures below -20°C, Rhee et al. (2005) maintained pollen viability for 1 year.

Once new hybrids are obtained, they can be propagated rapidly through in vitro culture. Various techniques have been studied and proposed, and very high propagation rates have been obtained. Takayama and Misawa (1983) used *L. speciosum* and *L. auratum*, and found that it was theoretically possible to obtain millions of bulblets in one year from one medium-size bulb. Thus, breeders have many effective techniques available for the propagation of new cultivars.

When evaluating the significant number of changes that have occurred in the past 50 years in the diversification of lily cultivars, it is apparent that the genus *Lilium* is an excellent example of an efficient exploitation of the genetic diversity through a combined utilization of improved knowledge and highly sophisticated techniques. In all probability, this will continue, and the use of advanced molecular approaches, including gene transfer, will make lily breeding even more efficient. A limiting factor could be that only a few countries and companies currently have lily breeding programs.

7. Narcissus. The genus consists of about 63 species, plus many subspecies and natural hybrids, and they primarily originate in the Iberian Peninsula and Europe (Wylie 1952; Hanks 1993). They were popular as early as the 16th century in the United Kingdom and in the Netherlands but did not become an important bulbous crop until the 19th century (Barr 1884; Doorenbos 1954; Hanks 1993). The breeding of Narcissi started between 1835 and 1855 in the United Kingdom and at the end of the 19th century in the Netherlands (Wylie 1952; Doorenbos 1954). The number of cultivars increased rapidly and characteristics such as plant vigor and the size, shape, and colors of the flowers were markedly improved (Kington 1989). These improvements were possible due to the high degree of variability in the genus, the ease of inter- and intraspecific crossings, and the development of polyploidy, mainly through the existence of unreduced gametes that are present in all groups of garden Narcissi (Wylie 1952; Doorenbos 1954).

Since 1955, the Royal Horticultural Society (UK) has published the registrations of all Narcissi cultivars. The Society is the International Registration Authority for Narcissi. The 1989 edition (Kington 1989) listed 23,000 names, which represented an estimated 18,000 cultivars (Hanks 1993). However, the number of commercially grown cultivars is considerably lower. In the season 2006–2007 (PT/BKD 2007), 1,734 ha were devoted to Narcissi bulb production in the Netherlands. About 480 cultivars were grown, but only a few were produced on significant acreages. It was reported that 595 ha of the total production was ‘Tête-à-Tête’, which is used primarily for a potted plant production (De Hertogh 1996). It is interesting to note that the double-flowered ‘Van Sion’, which was initially grown in the Netherlands in 1603, was produced on 3.65 ha during the 2006–2007 season (PT/BKD 2007).

Like other bulbous genera (e.g., tulips, hyacinths), the horticultural use of Narcissi evolved from the exclusive use as a garden plant to being forced either as fresh-cut flowers or potted plants. As far as breeding objectives are concerned, these uses led to additional requirements,

and specific research program were developed, mainly in the United Kingdom (Fry 1975). European cultivars and some selections raised in Australia produced early-flowering types. Breeding for resistance to basal rot (*Fusarium oxysporum* f. sp. *narcissi*) was also studied (Bowes 1992; Linfield 1992, 1997; Carder and Grant 2002). Some cultivars exhibited field resistance, but complete resistance was observed only in certain species.

In the first decades of the 20th century, one of the main objectives of Dutch breeders was breeding of yellow trumpet daffodils (Dix 1974b). The well-known 'Golden Harvest' (1927) is a cross between 'Golden Spur' and 'King Alfred'; however, this cultivar is susceptible to basal rot. In 1911, a mutant with a split corona was found. It was called 'Orchid daffodil', but later the name was changed to 'Buttonhole'. Split-corona daffodils were initially described by De Mol (1923). In 1928, the breeder J. Gerritsen also discovered a split corona in his seedlings and called it a collar daffodil. In 1969, the group of the "split corona" daffodils became a new division in the classified list of daffodils (Kington 1989).

The breeding of *N. tazetta* ("Paperwhites") in Israel initially resulted in release of a few cultivars, including well-known 'Ziva'. Recently, new cultivars 'Ariel', 'Nir', and 'Inbal', have been released for use in gardens and forced potted plant production. Currently, *N. tazetta* is the leading flower bulb under production in Israel. In 2005, about 25 million bulbs were exported for dry sales, home forcing, and potted plant production and cut-flower forcing (Kamenetsky 2005).

Propagation systems, including twin scaling and micropropagation, have been developed and assist in accelerating the release of new cultivars (Hanks 1993). Somatic embryogenesis and genetic transformation have been achieved in *N. pseudonarcissus* cultivars (Sage and Hammatt 2002).

8. Tulipa. The center of origin of the genus is located in Central Asia, extending from the region of Tien-Shan and Pamir-Alai to the north and northeast (Siberia, Mongolia, and China), south to Cashmere and India, and west to Afghanistan, Iran, the Caucasus, and Turkey (Hoog 1973). A classification of the genus by Hall (1940) was based on morphological and cytological characteristics. Subsequently, Botschantzeva (1982) published a comprehensive treatise on tulips. Recently, a revision of the genus *Tulipa* based on morphological and cytogenetical characteristics, crossing data, and data on the geographical distribution has been proposed by Van Raamsdonk et al. (1997). According to their analyses, the genus *Tulipa* includes about 55 species distributed in two

subgenera. *T. gesneriana*, which is related to garden tulips, is the most cultivated species.

Scientific research on tulip genetics and breeding started in Europe about 1960, almost 400 years after their introduction to Europe. In Germany, the research was focused on the heritability of traits such as bulb production (i.e., the number and weight of bulbs) and flower color (Horn and Wricke 1964; Horn 1971; Weber and Horn 1978). Subsequently, studies on tulip genetics and breeding were carried out primarily in the Netherlands, where numerous traits were investigated. The initial studies determined the chromosome number of a very large number of commercial cultivars and the possibility of the production of tetraploid plants (Zeilinga and Schouten 1968a,b). Eikelboom et al. (2001) have summarized the various techniques to produce tetraploids. Also, the production of $2n$ pollen has been reported in Japan by Okazaki (2005). Extensive programs also were developed to investigate the feasibility of breeding and selecting cultivars with characteristics of importance for bulb growers and flower producers. Special efforts were placed on disease resistance, mainly *Fusarium* and the tulip breaking virus (TBV). The research also addressed other aspects, including the transmission of the traits, the development of screening tests for the selection of resistant genotypes, and the evaluation of the characteristics of commercial cultivars (Van Eijk and Leegwater 1975; Van Eijk et al. 1978, 1979; Van Eijk and Eikelboom 1983, 1990; Romanov et al. 1991; Eikelboom et al. 1992). The studies showed that some resistance, especially for TBV, occurred in *T. fosteriana* (Eikelboom et al. 1992; Eikelboom and Straathof 1999).

The length of the juvenile phase, which is 5 to 6 years, is a major impediment to tulip breeding. By accelerating the yearly growth cycles, Fortanier (1971) was able to shorten the duration of the juvenile period. He found, however, that the acceleration led to a decrease in harvested bulb weight. Thus, research was directed toward the possibility of early selection by studying the correlations between flowering plants and juvenile plants. It was found that selection for *Fusarium* resistance during the juvenile phase was feasible (Van Eijk and Leegwater 1975), and this also was true for selection for forcing abilities (Van Eijk et al. 1983). In western France (Britanny), where climatic conditions are characterized by very mild winters, selection for forcing ability can be done in the field when the plants flower for the first time after being grown from seed (Le Nard 1977). This provides the possibility of evaluating characteristics of the flower (color and shape) in the first step of selection.

Research programs on use of the interspecific crosses in breeding for disease resistance and new aesthetic and physiological traits in garden tulips were developed in the Netherlands. They indicated that the possibilities of using interspecific crosses are limited (Van Eijk et al. 1991; Van Raamsdonk et al. 1995). Either inhibition or poor pollen tube growth is often observed (Kho and Baër 1971). To avoid this problem, various techniques, including in vitro techniques such as in vitro pollination, ovule culture, ovary-slice culture (Van Creij et al. 1992, 1999; Okazaki 2005), embryo culture and embryo rescue (Custers et al. 1992, 1995; Okazaki 2005), and hormone treatments (Van Creij et al. 1997), were investigated. Studies on in vitro propagation with the goal of accelerating the propagation of new cultivars and to provide the breeders with additional tools has been carried out mainly in Japan, Great Britain, France, and the Netherlands (De Hertogh and Le Nard 1993d). Although some positive results were obtained, they were genotype dependent. As a result, it was suggested that in vitro bulb production was often very low (Le Nard and Chanteloube 1992). Later, studies in the Netherlands combined stem segment in vitro culture with subsequent adventitious bud subculture, and propagation rates up to 6,000 bulblets after 2 years could be obtained (De Klerk et al. 2005). Currently, none of these techniques is used routinely in tulip breeding programs.

Embryos excised from mature seeds have expressed a high degree of reactivity in vitro (Aubert et al. 1986). The problem is that the genotype propagated in vitro is unknown. Thus, the technique is not valuable if a true to type propagation is the goal. However, embryo culture and especially the culture of immature embryos can be of interest for the interspecific hybridizations (Custers et al. 1992, 1995; Okazaki 2005).

The ability to regenerate tulips in vitro is necessary for breeders to take advantage of all the techniques that can be used in the major agricultural plants. For example, the production of haploid plants has not been perfected, even though some positive results have been published (Van den Bulk et al. 1994). The same situation exists for genetic transformation (Wilmink et al. 1995). Thus, improved systems must be developed for in vitro plant regeneration.

Due to the large size of the genome of tulips, the use of molecular markers is limited (Krens et al. 2004). However, the use of isozyme techniques permits the identification of tulip cultivars (Booy et al. 1993).

The vase life of the tulip is a trait that must be considered in a breeding program, and this characteristic is highly variable in the genus. A 4-year study using more than 300 cultivars and species demonstrated that flowers grown in the field and transferred to 20°C after harvest had

a vase life from 4 to over 10 days (Le Nard, unpublished results). Some species (e.g., *T. eichleri*, *T. fosteriana*, *T. greigii*, and *T. kaufmanniana*) had a short vase life (about 4 days), while most of the cultivars of the Darwin Hybrid Group (the result of crosses between *T. gesneriana* and *T. fosteriana*) had a vase life about 5 to 6 days. Studies on the possibilities of selection for keeping quality and the inheritance of flower color have been conducted in the Netherlands at the IVT (Van Eijk and Eikelboom 1976; Nieuwhof et al. 1988, 1990).

In spite of numerous limitations, many tulip breeding programs exist. New cultivars are released yearly, and over 1,500 have been registered during the last 10 years (Bodegom and Van Scheepen 2005). It must be noted that most of these cultivars were bred in the Netherlands, but a few have been bred in France (INRA), the Czech Republic, Japan, and Latvia (Bodegom and Van Scheepen 2005). The importance of mutations (mainly spontaneous) must not be overlooked. They represent about 25% of the new cultivars registered annually. This can be explained by the fact that the garden tulip, *T. gesneriana*, has a huge variability (Le Nard 1999). Thus, intraspecific hybridization remains a viable option for breeders. Research on disease resistance, bulb production, and forcing ability should be valuable not only to breeders but for the commercial tulip industry. The use of in vitro techniques and/or molecular tools could cause some economic problems since most of the tulip breeders are small companies.

In the Netherlands, 1,778 cultivars were grown for commercial bulb production during the 2006–2007 season (PT/BKD 2007; www.bloembollenkeuringsdienst.nl). However, only 18 cultivars are grown on more than 100 ha, and these cultivars represent about 31% of the total acreage (3,240 ha out of 10,071 ha). These major cultivars are used primarily for greenhouse forcing during winter as fresh-cut flowers. Most of the other cultivars are grown on smaller acreages, but this group also includes the new cultivars that ultimately will contribute to cultivar turnover.

9. Other Genera. Besides genera that comprise most of the worldwide bulb production, there are other ornamental geophytes that are of economic importance in the cut-flower and pot plant industries. Cut-flower statistics from the Netherlands showed that *Freesia*, *Alstroemeria*, *Hippeastrum*, and *Zantedeschia* were, respectively, the 8th, 10th, 11th, and 13th most important cut flowers at the flower auctions (www.vbn.nl 2006). *Anemone* and *Ranunculus* are two other important genera for cut-flower production, especially under Mediterranean climatic conditions (Umiel and Hagiladi 2004). Some of these genera also are

used for potted plant production (De Hertogh 1996). The commercial development of these genera has been supported by plant breeding programs, but most are relatively new ones.

Freesia, which is native to South Africa, was introduced into England about 1816, but interspecific hybridization started only in the beginning of the 20th century (Bryan 1989, 2002). Breeding programs were established in England, France, and the Netherlands, and they produced types with a wide range of flower colors and double flowers. A milestone was the production of tetraploid plants with large flowers (Sparnaay 1966). The possibilities of propagation by seed of these new cultivars was also studied by Sparnaay (1966), but vegetative multiplication generally is used (Imanishi 1993). Currently, *Freesia* breeding is being conducted by private companies and mainly in the Netherlands.

Alstroemeria species originate in Chile, Peru, and Brazil (Bridgen 1993; De Jeu et al. 1992). Commercial breeding for greenhouse cut-flower production was initiated in England about 1948 (Przybyla 1992). Later, breeding was started in the Netherlands, and numerous interspecific hybrids combining important characteristics, such as year-round flowering, plant habits for cut flower or potted plant forcing, long flowering periods, a range of flower colors and shapes, and the ability to be increased by in vitro propagation, have been obtained (De Jeu et al. 1992; Bridgen et al. 2002). *Alstroemeria* breeding was enhanced by the production of tetraploid plants and by various in vitro techniques (De Jeu et al. 1992; De Jeu 2000; Bridgen et al. 2002).

Hippeastrum consists of about 60 species that are concentrated in two areas of diversification: eastern Brazil and the central southern Andes of Peru, Bolivia, and Argentina (Meerow et al. 1992a; Okubo 1993). Interspecific hybridizations, using a very limited number of species, have produced large-flowered, tetraploid hybrids. In order to enlarge the genetic diversity of the commercial material, breeding at the diploid level has been achieved (Meerow et al. 1992a). In general, the breeding programs have been conducted primarily by private companies in the United States, the Netherlands, and South Africa. These programs have produced a large number of cultivars expressing a great diversity in the types of flower (colors and shapes) and stem length. A new program on *Hippeastrum* hybridization, using wild relatives and embryo rescue in vitro techniques, currently is being developed in Israel (Sandler-Ziv et al. 2004).

Zantedeschia consists of a few species native to Africa (Funnell 1993; Singh 1996; Singh et al. 1996). The species are distributed into two groups that differ by their type of growth. One species, *Z. aethiopica*, is an evergreen plant producing white flowers in winter and spring. The second group includes about 8 species and subspecies that are

deciduous and summer flowering, and produce colored flowers ranging from pink and dark maroon to yellow (Funnell 1993). Active breeding programs concerning the species of the second group, and including interspecific hybridizations, started in the 1980s in New Zealand and resulted in a large number of commercial cultivars (Funnell 1993). The major objectives were a large number of flowers per tuber and diversity in flower colors. In vitro techniques, including embryo culture and tissue culture for rapid propagation, were developed (Funnell 1993). Breeding by Dutch companies started in the 1990s. Breeding for soft-rot [*Pectobacterium* (*Erwinia*) *carotovorum*] resistance is a major goal, but no definitive results have been obtained (Snijder and Van Tuyl 2002; Snijder 2004; Snijder et al. 2004).

Anemone and *Ranunculus* are native to Middle East and were introduced into Europe during the Crusades. Generally, they are seed propagated, and the tubers and tuberous roots are marketed for use in gardens or for a cut-flower or potted plant production (De Hertogh 1996). The genus *Anemone* consists of only a few species and subspecies (Meynet 1993a). Two are produced on a commercial scale: *A. blanda* is produced in the Netherlands for use as garden plant or potted plant. In contrast, the production of *A. coronaria* is concentrated in Israel, the Mediterranean, and cool oceanic regions of western Europe and the United States. They are used mainly as cut flowers. Active breeding work for cut-flower usage has been conducted in the United States, the Netherlands, and more recently in France and Israel. The major goals are: (1) the selection of cultivars adapted to an autumn–winter cutflower production under Mediterranean climatic conditions; (2) an improvement of plant vigor; and (3) an increase in flower types and colors. Breeding has some limitations due to the failure of interspecific hybridizations and the limited use of biotechnological tools. An important step, however, was the production of tetraploid plants. Currently, several cultivars exhibiting various levels of ploidy (di-, tri- and tetraploids), and expressing a great diversity in flower color and shape exists. At the diploid level, Israeli selections such as ‘Jerusalem’ and ‘Meron’, whose parentage includes indigenous anemones, are among the most popular. Tetraploid cultivars (e.g., French selections such as ‘Tetranémone’ and ‘Marianne’) are generally more vigorous, but flower later and produce fewer flowers per plant. The most recent French selections are triploid. The Israeli selections ‘Galilee’ and ‘Carmel’ have had commercial success. These new cultivars have contributed to the development of winter cut-flower production in the Mediterranean region. The same cultivars can be used for spring cut-flower production in the Netherlands, but in this case plants produced from seeds are used.

Ranunculus asiaticus is the only species cultivated for its ornamental characteristics. It was widely grown in the Mediterranean areas and in the cool oceanic areas of Western Europe (Flanders, England) in the 18th and 19th centuries (Meynet 1993b). The species can be used not only as garden plants but also as cut flowers, because it is winter flowering and has long stems and attractive and -ong lasting flowers. Pot plant production is also possible because genetically short-stemmed types exist, and plant growth retardants (PGRs) can be applied (De Hertogh 1996). Since *R. asiaticus* has some auto-incompatibility and is susceptible to inbreeding, commercial cultivars are mostly hybrids (Meynet 1993a). By using the sib mating technique, genetic, homogeneous material can be obtained, and cultivars exhibiting homogeneous colors are available. The production of true F_1 hybrids should be possible through the use of double haploids issued from anther in vitro culture (Meynet and Duclos 1990a). However, since the double haploid plants have a low vigor, seed production is still a major problem. Anther in vitro culture has also produced a large somaclonal variation through somatic embryos, and the new characteristics, especially colors, appeared stable and were transmitted as nuclear mutations (Meynet and Duclos 1990b). Recently, flower types with green centers have been obtained. This occurred because with some genetic types, the ovaries can produce leaf- or bractlike organs. In general, breeding programs with *Ranunculus* has been carried out either by small research teams or private companies in France, Italy, Japan, Israel, and the United States. These programs have released a wide range of cultivars that are propagated primarily by seed. The exceptions are the recent Italian cultivars, which have been vegetatively propagated through in vitro culture.

B. Physiology

De Hertogh and Le Nard (1993b) and their colleagues have provided a comprehensive treatise on the physiology of flower bulbs. In addition, Rees (1972, 1992) has published two books on bulb physiology. Thus, this part reviews only the research reports that significantly impacted the successful globalization of the flower bulb industry. In addition, only bulb production and bulb forcing are covered, because they have had the major economic impacts (De Vroomen 1993). Garden and landscaping make up the third important market for flower bulbs but this area tends to underutilize the bank of research knowledge.

1. Bulb Production. The goal of all bulb growers must be to produce disease-, insect- and physiological disorder-free bulbs that flower

successfully in the marketplace. To assist bulb growers, many production guides have been published (e.g., Gould 1957; Krabbendam and Baardse 1966a,b; 1967, 1968a,b; 1972a,b; Kiplinger and Langhans 1967; Schenk 1968, 1972; Wallis and Mather 1977; Vijverberg 1980; Moore 1984; ADAS 1985a; Gilbert 1985; Smith and Danks 1985; Bouwman et al. 1988; Van Brenk 1988; Van Nes and Komijn 1988; Van Nes 1989, 1991; Zwart 1989; Miller 1992; and Rouwette et al. 2004). These publications cover an extensive number of flower bulbs but, most likely, will not be updated due to reductions in public funding for flower bulb research and technology transfer. A key factor for the production of high-quality bulbs is to know the growth and developmental cycle and flowering requirements of each species and the large number of cultivars that are available (Zandbergen 1980; Leslie 1982; Van Scheepen 1991, 1996; Kington 1998; Bodegom and Van Scheepen 2005; IBC 2006, 2007; Matthews 2007a,b). This knowledge is important because of their widely different agronomic requirements. For example, some tulip cultivars have higher yields in sandy soils, while others perform best in clay-based soils (Schenk 1968, 1972). Fig. 1.4 illustrates the complexity and interactions of the major factors affecting bulb yield. The requirements of each species and/or cultivar must be considered by the growers to maximize profitability through high bulb quality production.

The propagation techniques used by the growers vary by bulb type and sometimes the cultivar selection. The two basic techniques that are

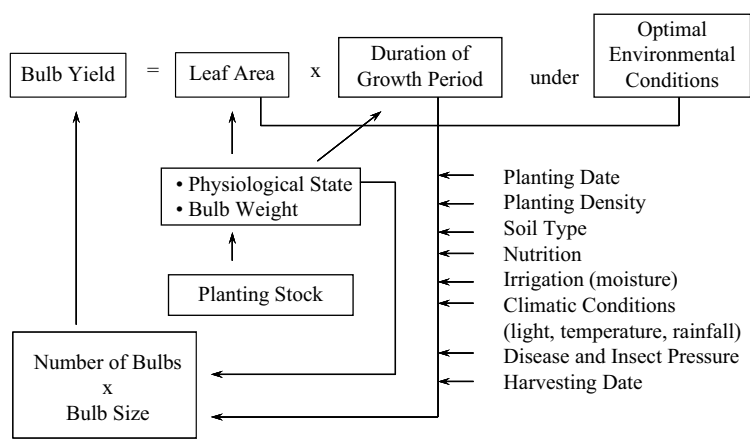


Fig. 1.4. Schematic relationships of the major factors affecting plant growth and bulb production of ornamental geophytes (Le Nard and De Hertogh 2002).

widely used are sexual and asexual (Le Nard and De Hertogh 2002). The latter is the most prevalent system for flower bulbs in order to retain the horticultural characteristics of the cultivars. In all cases, the factors that must be controlled affect either flower development and/or serious pests, such as yellow disease of hyacinths. For sexual reproduction, it is important to know the storage and germination requirements of the seed. Although sexual reproduction is used mainly for plant breeding (see Section IV.B), it is also used for some commercially produced ornamental geophytes (e.g., some *Alliums*, tuberous begonias, some lilies, and *Ranunculus*; Zwart 1989; De Hertogh and Le Nard 1993d).

Asexual techniques use either naturally occurring systems or artificially developed systems (Table 1.6). For all asexual techniques, it is critical to use clean stock, which may involve tissue culture to eliminate diseases such as viruses (Kim and De Hertogh 1997).

Flower bulb production systems utilize greenhouses (e.g., Dahlias, Freesias, and lilies) and/or outdoor fields. For the latter, it is essential to use minimum 5-year field rotations in order to reduce disease pressure. The basic factors to consider for outdoor production are described in Table 1.7. All bulb production systems require highly specialized facilities and equipment. They include specialized bulb storage buildings equipped with precise control of temperature (a range of -2° to 44°C), ventilation, and sometimes relative humidity (Bouwman 1988).

Table 1.6. Examples of asexual propagation systems for ornamental geophytes.

System	Propagation Systems	Example
Naturally occurring	Annual replacement	Tulips and cormous species
	Perennial mother bulb	Hyacinths and <i>Hippeastrum</i>
	Runner type	Rhizomatous Irises and <i>Convallaria</i>
	Stem bulblets	Lilies
	Scale bulblets	Lilies
	Aerial bulblets (bulbils)	Lilies and Tulips
	Leaf cuttings	<i>Lachenalia</i>
Artificial propagation	Sectioning of selected mother bulbs	Lilies
	Scooping and scoring of selected mother bulbs	Hyacinths
	Cuttings	Dahlias
	Chipping and twin-scaling	<i>Narcissus</i> and <i>Hippeastrum</i>
	Leaf cuttings	<i>Lachenalia</i>
	Use of daughter bulbs of forced plants	Tulips
	Tissue culture	Lilies

Table 1.7. Critical factors for outdoor bulb production
(De Hertogh and Le Nard 1993d).

Selection of either the bed or row planting system
Selection of planting times, depths (based on bulb hardiness), and densities
Agronomic factors
Soil requirements
Drainage
Nutrients levels
Irrigation systems
Winter protection systems
Systems to control of foliar diseases and insects
Control of weeds (especially species like <i>Nasturtium silvestre</i> —“Kiek”)
Roguing and required field inspections
Flower deheading system to be used
Harvesting times (based on physiological maturity of the bulbs)

The precise conditions vary with the bulbs being produced. Needless to say, these facilities have changed greatly over the years, as illustrated by Popma (1998) and the Werkgroep Bollenschuren (2003). Examples of necessary highly specialized equipment include:

- Hot water treatment (HWT) facilities
- Planting machines
- Sprayers
- Flower deheaders
- Bulb harvesters
- Bulb washing facilities to remove soil from bulbs for export to certain countries (e.g., the United States and Canada)
- Bulb drying facilities
- Tulip bulb peeling equipment
- Bulb graders and counters.

The postharvest bulb handling systems must be designed to select high-quality planting and marketing stocks, proper packing materials for each bulb type, and the mode (air, sea, or ground) and optimal period for transportation of the bulbs to the marketplace (De Hertogh and Le Nard 2004).

2. Bulb Forcing and the Flowering Process. Broadly defined, flower bulb forcing is “the flowering of a bulb using other than naturally occurring conditions.” Thus, one of the earliest types of forcing was to plant hyacinths between greenhouses in order to have them flower earlier than in the open fields (Blaauw and Kronenberg 1937). In 1910,

Nicolaas Dames developed the system for early lifting of Dutch-grown hyacinths to “prepare” them for very early forcing in greenhouses, a system that still is used today (Dwarswaard 2006). Subsequently, in the 1920s to 1960s, Professor. Blaauw and his colleagues investigated 23 different genera and cultivars and developed the essential requirements for forcing of flower bulbs (Blaauw 1920; Hartsema 1961; Hartsema and Luyten 1962).

The principles of controlling flowering in flower bulbs and the utilization of the knowledge for commercial forcing have been reviewed by De Hertogh (1974), Le Nard and De Hertogh (1993a), and Theron and De Hertogh (2001). As with flower bulb production, many forcing guides are available for commercial bulb forcers (De Pagter 1972; Buschman and Roozen 1980; Anon, 1981; ADAS 1983, 1985b; De Hertogh 1996; Van den Hoek and Jonkheer 1968). Flower bulb forcing has been divided into five phases: (1) production, (2) programming, (3) greenhouse, (4) marketing, and (5) consumer. All of them are important and are closely linked, but, without question, consumer satisfaction is by far the most critical phase. Forcing is controlled by genetic and environmental factors. As reported by Blaauw and his colleagues (Hartsema 1961), temperature is the most important factor. It affects the time and rate of flower initiation and development, which is critical for commercial forcing that must meet market demands. A significant development was the establishment of “cold-week” requirements for bulbs like tulips (Rees and Turquand 1969; De Hertogh 1970). This part of the programming phase allows forcers to schedule the cultivars for specific market dates, such as Valentine’s Day (14 February) and uses, such as fresh-cut flowers or flowering potted plants, both of which have highly different marketable height requirements. In addition, this system dispelled the concept that bulbs are ready to bring into the greenhouse when the shoots emerge from the bulb noses. It was found that there was no correlation between emerged shoot length and the ability to be forced. It was also shown that there was no absolute correlation between the stage of flower bud differentiation and the physiological state of the bulbs that determines the subsequent growth capacity of the (daughter) plants (Le Nard and De Hertogh 1993a). In fact, there are two important seasonal physiological processes: (1) physiological maturity of the bulbs and (2) the state of dormancy, which is, in reality, a period of intrabulb development (Kamenetsky 1994). Within bulb lots, there are population effects due to variations in planting depth positions within the bed, row orientation in the field, and normal plant population variability.

As with bulb production, forcing requires specialized facilities and equipment, which have undergone many changes over time. Early and inexpensive forcing facilities for spring-flowering bulbs included:

- Outdoor rooting beds
- Cold frames
- Plastic hoops
- Non-temperature controlled bulb cellars (Anon, 1963)

Subsequently, controlled-temperature rooting rooms for spring-flowering bulbs, specialized facilities to freeze-in lily bulbs and retard Dutch *Iris* bulbs, greenhouses with rolling benches, hydroponic systems for cut tulips, and even Australian greenhouses with retractable sides or roofs have been developed and are being used extensively. Thus, bulb forcing has become a global business based on an extensive scientific database.

De Hertogh (1996) has divided the forcing systems into two basic types: controlled temperature rooting room forcing, which is based on Professor Blaauw's research (Hartsema 1961) and includes many spring-flowering bulbs, such as tulips, hyacinths, daffodils, and hydroponic tulips; and non-rooting room bulbs, which includes special precooling (SPC) (at 5°C) tulips (which have declined significantly in recent years), freesias, *Hippeastrum*, and lilies. With bulbs like Dutch irises and lilies, the two systems can be partially combined. Thus, after being programmed, the bulbs are planted in trays, rooted in controlled temperature rooting rooms, and then placed in greenhouses.

Flower bulb forcing is global and its uses vary by country. The three keys to success involve knowledge that:

1. Each bulb has specific requirements for forcing
2. Each bulb production season is different
3. There are important production carry-over effects

Consequently, bulb forcers must conduct periodic and timely inspections throughout the forcing season. Last, as Le Nard and Cohat (1968) have reported, tulips exhibit a strong competition between bulbing and flowering. During forcing, the goal must be to control both processes and prevent flower abortions after the flower(s) is initiated. In this area, another technique to minimize flower abortion in tulips is to use an in-between temperature of 17°C for 1 to 6 weeks (the duration is cultivar dependent) before precooling tulips for early forcing (De Hertogh 1996; J. van den Hoek 1991, pers. comm.).

3. Morpho- and Physiological Aspects of Florogenesis. Florogenesis in ornamental geophytes can be divided into five consecutive steps: induction, initiation, organogenesis (differentiation), maturation and growth of floral organs, and anthesis¹ (Halevy 1990; Bernier et al. 1993; Le Nard and De Hertogh 1993a). The induction of flowering is affected markedly by the genetics of the individual plant species and environmental factors. Interactions between these factors affect a series of molecular and biochemical processes leading to the transition of the plant from vegetative to reproductive development (Flaishman and Kamenetsky 2006). During flower initiation, the vegetative meristem terminates leaf production and shifts to reproductive development. Flower differentiation involves the formation (organogenesis) of the inflorescence, composed of individual flowers and flower organs, while flower maturation consists of growth of flower organs, differentiation of sporogenous tissues in the anthers, meiosis, and pollen and embryo sac development. The process is terminated by anthesis.

Many bulbous species, such as hyacinths, develop a multiflowered inflorescence. During inflorescence formation, the shoot apical meristem undergoes several significant steps, from transition to the reproductive stage to initiation of the first flowers and flower-bearing bracts (Table 1.8).

In the Alliaceae, Amaryllidaceae, and Liliaceae, the perianth is the first floral organ formed (Table 1.8; Waterschoot 1927; Blaauw 1931; Le Nard and De Hertogh 1993a; Kamenetsky and Rabinowitch 2002). In contrast, in Dutch irises, the first floral organs to be formed after initiation are the stamens A_1 (Cremer et al. 1974).

Tulipa. Because of the economic importance of tulips, this review summarizes only the salient research on them conducted by Professor Blaauw's group. Previously, the physiology was summarized by De Hertogh et al. (1983) and Le Nard and De Hertogh (1993c). It must be pointed out that the first illustration of flower development in tulips was provided by Grew (1682). Subsequently, about 250 years later, Mulder and Luyten (1928) examined flower formation during environmentally controlled dry storage of tulip bulbs. They found that bulbs for early forcing could be stored at 5°C or 9°C for a specified numbers of weeks (Beijer 1942). Blaauw and Versluys (1925) and Blaauw (1926) also found that bulbs could be precooled at 5°C, but, in some cultivars, flower abortion occurred. This and other research has led not only to the commercial precooling of bulbs for early standard bulb forcing but also for the SPC (5°C) system (De Hertogh 1996). Blaauw and his

¹Anthesis is the opening of the flower bud or flowering.

Table 1.8. Abbreviations assigned to floral stages during inflorescence and flower development in bulbous species of Liliaceae and Amaryllidaceae (after Blaauw 1931; Beijer 1942; Le Nard and De Hertogh 1993).

Stage symbol	Developmental stages of inflorescence and individual flower
I	Vegetative apical meristem—leaf forming stage
II	Transition to reproductive stage—doming of apex prior to flower initiation (Prefloral stage)
Sp	Spathe initiation
Pr	Appearance of primordia of first flowers
Br	Appearance of initials of flower-bearing bracts or specialized leaves
Bo	Secondary bracts
P ₁	Formation of first whorl of perianth (tepals)
P ₂	Formation of second whorl of perianth (tepals)
A ₁	Formation of first whorl of androecia (stamens)
A ₂	Formation of second whorl of androecia (stamens)
G	Formation of trilobed gynoecium (pistil)
G +	Style is distinct and lobes are discernible
Pc	Paracorolla (e.g., trumpet of <i>Narcissus</i>)

coworkers suggested that the length of the shoot should be used as the criterion for changes in temperature, but, subsequently this was found to be unreliable. Currently temperature changes are based on the number of cold-weeks at a certain temperature. It is known that cultivars have an optimum, minimum, and maximum number of weeks for determined forcing conditions (Van den Hoek 1991, De Hertogh 1996). Freezing temperatures ($-1/2^{\circ}\text{C}$) can delay flower formation, and this temperature range has been used for storage of tulips for growing and forcing in the southern hemisphere (Blaauw et al. 1930; Hartsema and Blaauw 1935). Currently, however, there is adequate tulip bulb production in the southern hemisphere (Table 1.2). Very often, the daughter bulbs of plants forced in the northern hemisphere are used as planting material in these countries. Thus, specialized long-term storage treatment is not required.

The precise number of floral organs formed by a tulip flower (Table 1.8) is influenced by the temperatures used for bulb storage (Blaauw et al. 1932). They found that the fewest number of abnormalities occurred at 17–20°C. To increase the bulb yield and the number of large-size bulbs, especially the central bulb, the method of “blindstoken” was developed (Hartsema and Luyten 1950). This method employs high temperatures in the very late summer to abort the flower within the bulb, but is not used in practice, because in order to ensure bulb quality, the flowers must be inspected for viruses and true-to-type characteristics.

Hyacinthus. The process of flowering in hyacinths has been examined in detail since 1900. At this time, it was known that hyacinths grown near Berlin, Germany, and in the south of France flowered earlier than hyacinths grown in the Netherlands. Moerlands (1915) has summarized the temperature treatments that were developed by Nicolaas Dames in 1910 for early forcing. Blaauw (1920) provided the initial in-depth study of the periodicity of the hyacinth (i.e., leaf formation, flower formation, growth of floral stalk and inflorescence, and the rest period). He concluded that there is no true dormancy period within the bulb. Flower formation required a minimum of four leaves and relatively high temperatures (Blaauw 1923b; 1924a,b). Versluys (1925) described the development of the hyacinth with sheath and foliage leaves and found that longest period of active growth was in the basal zones of the leaves, and that growth ceased basipetally. Subsequently, Luyten (1926b) showed that cell division was temperature dependent. Blaauw 1920 showed that long storage at 35°C resulted in shorter-foliage leaves. However, storage at 35°C followed by 17°C caused an increase in cell division and longer-foliage leaves. Versluys (1927) found that root formation started in the middle of May in the field and terminated in October and is very temperature dependent. She found that a soil temperature of 17°C enhanced root growth.

Luyten et al. (1932) were able to advance intrabulb flower formation. They found that the optimal temperature for flower formation was 25°C and that no flower formation was observed at 34°C. After the upper florets of the inflorescence reached Stage P₁, 17°C must be maintained until all flowers reach Stage G. This prevents the physiological disorders green tops and dry flowers that are caused by partial or complete flower abortion. Flower formation is affected not only by storage temperatures but also by the environmental conditions of the production area. Thus, hyacinths grown in southern France formed flowers approximately one month earlier than those grown in the Netherlands, due to higher growing temperatures (Blaauw and Kronenberg 1937). Flower formation can be delayed by storage at 2°C to 4°C and 28°C as long as the flowers are in Stage P (Hartsema and Waterschoot 1939; Table 1.8). Nowak and Rudnicki (1993) have produced an extensive review of the physiology of hyacinths.

Narcissus (Daffodils). The initial studies on Narcissi were conducted with ‘King Alfred’, which was popular in the beginning of 20th century. In 2007, however, this cultivar was produced on only 0.07 hectare in the Netherlands (PT/BKD 2008). Flower initiation occurred in ‘King Alfred’ during the spring and was almost complete at the time of bulb harvest

(Huisman and Hartsema 1933). In comparison to the tulip and hyacinth, the daffodil has two additional stages of flower formation (Table 1.8). If the bulbs are lifted when apical meristem has reached only Stage I (the initiation of scales and leaves), it will not initiate a flower. This is very different from the hyacinth but is similar to the tulip. Thus, if Stage Sp has been reached prior to lifting of the bulbs, flower formation and/or flower development can be precisely controlled by the postharvest storage temperatures (Gerritsen and Van der Kloot 1936). Normally, the flowers in bulbs lifted at the end of July or beginning of August in the Netherlands are in Stage G. Hartsema and Blaauw (1935) found that storage at 25°C–31°C for 16 weeks delayed flowering, while temperatures above 31°C or between $-1\frac{1}{2}$ °C and 5°C induced flower abortion. Providing a 9°C temperature directly after lifting causes dwarf growth (Van Slogteren 1933), but this physiological disorder can be avoided by an initial storage at 18°C for 2 weeks directly after lifting and then using 9°C. Hanks (1993) has produced an extensive review of the physiology and production of *Narcissi*.

Iris (Bulbous). Many aspects of flower formation and development, including descriptions of the different stages of flower development, the effects of storage temperatures and light requirements for forcing of the bulbous irises ‘Imperator’ and ‘Wedgwood’, were investigated by Blaauw and his coworkers (Blaauw 1935; Dix 1974a). They also compared leaf and flower formation of Spanish, English, and Dutch irises in the field. Van der Meulen and Luyten (1936) found that in the Netherlands the Dutch iris reached Stage G earlier than the Spanish and English irises, and this resulted in earlier flowering. Blaauw (1933) reported that in the Netherlands ‘Imperator’ bulbs were in Stage I at planting time, and flower formation had reached Stage G at the beginning of April with flowering occurring in June. Flower formation required 7°C to 9°C, and maintaining higher or lower temperatures for a long period delayed flower formation (Blaauw 1934, 1941). The forcing ability of ‘Imperator’ depended on the bulb size and required approximately 150 days. Hartsema and Luyten (1953, 1955) found that the percent of flowering bulbs was dependent on the temperature treatments and the number of days of supplement light and the light intensity. Higher-flowering percentages were obtained when supplementary lighting started 40 to 50 days before the predicted date of flowering (Hartsema and Luyten 1953).

Iris reticulata (a dwarf *Iris*) differs greatly from tall growing Dutch *Iris*. In the field, flowering occurs from the end of February to the end of March. Like the tulip, flower formation occurred inside of the bulb after lifting and during dry storage. At planting, all bulbs must be or have

been in Stage G (Luyten 1935). The physiology and production of bulbous Irises have been reviewed in detail by De Munk and Schipper (1993).

Gladiolus. Hartsema (1937) used the late-flowering cultivar 'Vesuvius' for growth and developmental studies. She found that flower formation was initiated after planting of the corms in April and was dependent on the soil temperature, with 13°C being optimal for flower formation in the Netherlands. Two types of roots were observed. The regular roots were differentiated during dry storage of the corms and emerged immediately after planting. The contractile roots were developed in tissue located between the old and new corms, and they were observed after mid-May. The physiological studies of Gladioli have been reviewed in detailed by Cohat (1993).

Hippeastrum (Commercially called *Amaryllis*). The perennial bulb of the *Hippeastrum* hybrids is composed of enlarged leaf sheaths (Okubo 1993; Theron and De Hertogh 2001), and the number of apical shoot units depends on the bulb size (Blaauw 1931; Okubo 1993). Each unit consists of three complete round scales, a half scale, and an inflorescence. Blaauw (1931) found that flower formation occurred throughout the growing period. The terminology for flower formation in *Hippeastrum* has been divided into 11 stages by Blaauw (1931) and Beijer (1942). Since several flower stalks are initiated in the bulb, *Hippeastrum* can simultaneously produce more than one flower stalk, which is a desirable trait for forcing. Blaauw (1931) found that the second stalk is generally longer than the first. In the northern hemisphere, the forcing of *Hippeastrum* depends on the market. Normally, it starts in November and continues to the end of March. Up to 1926, most of the *Hippeastrum* were propagated by seed. Subsequently, Luyten (1926a, 1936) developed a system partly based on scooping (i.e., removing the bulb disc and separating the scales). Currently, propagation is asexually using either offsets or twin-scaling techniques. Okubo (1993) and Theron and De Hertogh (2001) have produced reviews of the physiology and production of *Hippeastrum*.

4. Molecular Aspects of Florogenesis. In spite of the fact that information on physiological mechanisms of floral transition of bulbous species is extensive, the molecular aspects of this process in ornamental geophytes are not understood. The paradigm from model plants (e.g., *Arabidopsis*) suggests that the transition of the shoot apical meristem from the vegetative to the reproductive phase is controlled

by a large group of flowering-time genes (Corbesier and Coupland 2006; Kanno et al. 2007). This process is controlled by endogenous and environmental signals, including photoperiod and temperature and plant hormones. The signals from the various flowering-time pathways are integrated and lead to the activation of a small group of floral integrators—genes that specify floral identity (Benlloch et al. 2007). The meristem identity-genes—*APETALA1* (*AP1*) and *LEAFY* (*LFY*)—activate the floral-organ identity-genes, which specify the various floral cell types and tissues, including sepals, petals, stamens, and carpels (Zik and Irish 2003; Bernier and Perilleux 2005; Moon et al. 2005; Benlloch et al. 2007; Corbesier et al. 2007; Kanno et al. 2007). Recently, *LFY* homologues were also identified in some geophytes: for example, *Narcissus tazetta* (*NLF*; Noy-Porat et al. 2007), garlic (*gaLFY*; Rotem et al. 2007), and the Madonna lily, *Lilium candidum* (*LcLFY*; Zaccai et al. 2008).

Most ornamental geophytes belong to the monocot botanical order *Liliales* and form flowers with 6 perianth lobes (tepals), arranged in outer and inner whorls, 6 stamens, and a tricarpellary pistil situated in the center of the flower (Table 1.8). This arrangement is different from dicots, including the most popular model species *Arabidopsis thaliana* and *Antirrhinum majus*, in which the floral organs are arranged in 4 concentric whorls, carrying inwardly sepals, petals, stamens and carpels, respectively (Fig. 1.5). Following genetic and molecular analyses, the genetic control of floral organ identity in the model plants was explained by the ABC model (Coen and Meyerowitz 1991). The model proposes that class A, B, and C organ-identity genes act in overlapping domains to determine the flower pattern (Fig. 1.5). Accordingly, the expression of class A genes specifies sepal and petal determination, the combination of class A and B genes specifies the formation of petals in the second whorl, the class B and C genes specifies stamen formation in the third whorl, and the expression of the class C genes alone determines the formation of carpels in the fourth whorl.

Van Tunen et al. (1993) proposed a modified ABC model for tulips (*Tulipa gesneriana*), in which the expression of B-class genes is extended to the first floral whorl (Fig. 1.5b). Further studies in geophytes, such as tulip (Kanno et al. 2003), *Agapanthus praecox* (Nakamura et al. 2005), *Muscari armeniacum* (Nakada et al. 2006), and the orchids *Phalaenopsis equestris* (Tsai et al. 2004, 2005) and *Dendrobium crumenatum* (Xu et al. 2006), supported this model. In addition to being expressed in monocots, the AP3 and PI class B gene homologues are expressed in petaloid sepals in the first whorl in 2 dicots, *Aquilegia alpina* of Ranunculaceae (Kramer et al. 2003). The expansion of class B gene

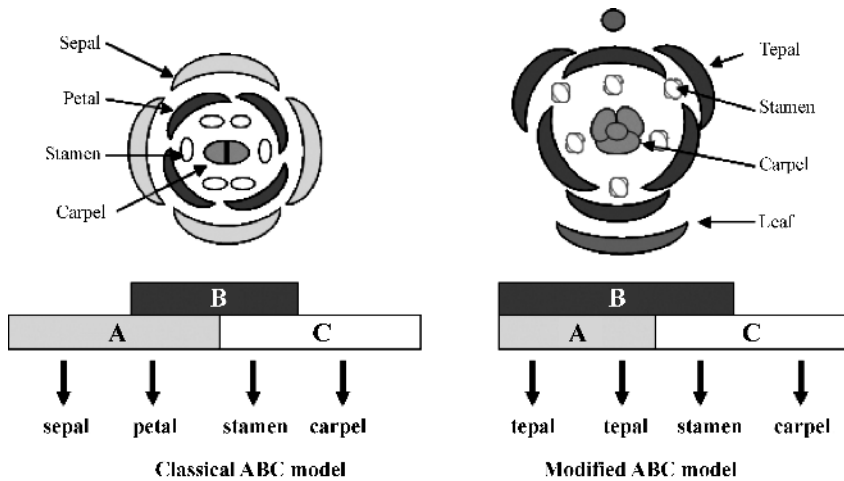


Fig. 1.5. Flower structures of the model species *Arabidopsis* (a) compared with typical representatives of ornamental geophyte *Tulipa* (b). Note presence of two separate whorls of sepals and petals in the model dicots, while in monocots the perianth lobes are presented by two whorls of tepals. Classical and modified ABC model (after van Tunen et al. 1993) suggests that in higher eudicots (e.g., *Arabidopsis thaliana*), expression of A-function genes specifies sepal formation in the whorl 1, the combination of A- and B-function genes specifies the formation of petals in whorl 2, B- and C-function genes specify stamen formation in whorl 3, and expression of a C-function alone determines the formation of carpels in whorl 4. In *Tulipa*, expression of A-function genes specifies tepal formation in the whorls 1 and 2. Class B genes are expressed in whorls 1, 2 and 3; B- and C-function genes specify stamen formation in whorl 3 and expression of a C-function determines the whorl 4.

expression into the first whorl is consistent with the floral morphology of these species.

Recently, the ABC model was extended to the ABCDE model (Theissen 2001). Whereas the E-function genes together with the B and C genes control stamen formation, the C- and E-function genes regulates carpel formation and the D-function genes are involved in ovule development. In *Lilium longiflorum*, *LMADS2*, a new MADS-box gene form, was described as a D-functional gene (Tzeng et al. 2002) on the basis of sequence comparison and phylogenetic analysis. *LMADS2* is specifically expressed in the lily carpels. E-function-related genes *LMADS3* and *LMADS4* were characterized from *L. longiflorum* (Tzeng et al. 2003). Both *LMADS3* and *LMADS4* mRNAs were detected in the inflorescence meristem, in floral buds at different developmental stages, and in all 4 whorls of the flower organs (Benedito et al. 2004b). These characteristics of *LMADS2*, *LMADS3*, and *LMADS4* provide useful information on

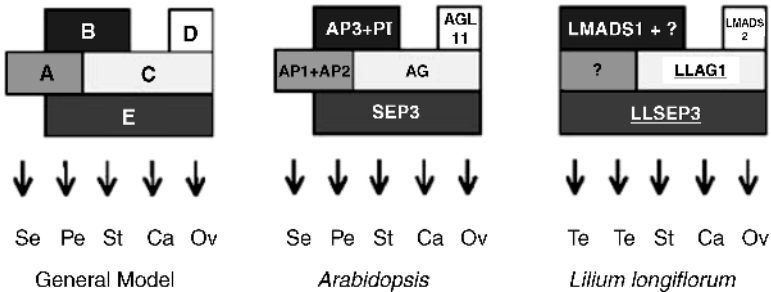


Fig. 1.6. The ABCDE model for flower development. The general ABCDE model states that five genetic functions act in an overlapping fashion in order to trigger the development of floral organs. Genes of each function were found in the model species *Arabidopsis*, and some of the ABCDE functions have been already characterized in *Lilium longiflorum*. From: Benedito et al. 2004b, with permission. Abbreviations: Se, sepals; Pe, petals; St, stamens; Ca, carpel; Ov, ovules; Te, tepals.

the relationships between the C- and D-functional MADS-box genes and E-function MADS-box genes in lily flower development and help the establishment of ABCDE flowering model in *L. longiflorum* (Fig. 1.6).

These data indicate that in ornamental geophytes, flower development may be controlled differently than in the classical model plants such as *Arabidopsis* (i.e., in a modified ABCDE model). In addition, the model suggested by Van Tunen et al. (1993) may not be applicable to other species from the *Liliales* families. Clearly, more research remains to be done to understand the floral organ identity genes in ornamental geophyte species.

C. Pests, Physiological Disorders, and Plant Growth Regulators

1. General Aspects for Best Management Practices. As previously stated (see Section IV.C.2), the goal of all flower bulb growers must be to produce bulbs that are free from all major diseases and insects (pests) and will flower at desired time without physiological disorders. To accomplish this goal, bulb growers, forcers, and gardeners must focus on problem prevention through the utilization of knowledge (de Boer 2008). Six of the key factors to utilize for best management practices are listed next.

1. Use clean planting stock.
2. Implement all integrated pest management practices.
3. Employ pesticides properly and in a limited manner.

4. Conduct all required inspections.
5. Control environmental factors affecting the crop.
6. Diagnose problems properly.

The industry is fortunate that in the 20th century, the accumulated scientific knowledge on pests and PGRs is available in many publications: for example, Gould and Byther (1979a,b,c); Moore et al. (1979); Baker (1982, 1993); Bergman (1983); Lane (1984); ADAS (1986); Byther and Chastagner (1993); Van Keulen and Van Aartrijk (1993); and Van Aartrijk (1995). Also, modified atmosphere packaging (MAP) or controlled atmospheres (CA) can be used for prolonged storage of flower bulbs during transportation (Droby et al. 1997; Philosoph-Hadas et al. 1997, 1999). In addition, the occurrence of serious diseases was largely responsible for the establishment of the LBO in Lisse and the BKD in Hillegom, the Netherlands (see Section V.C.1). Their scientists have provided not only valuable research but also diagnostic tools and services. Many sources, including the North Carolina Agricultural Chemical Manual (2008), are available on the web and provide pest control information.

2. Diseases of Ornamental Geophytes. Byther and Chastagner (1993) have reviewed the groups of diseases that affect flower bulbs. Besides the four major types described here, a mycoplasma that occurs from time to time causes lisser disease in hyacinths. When this occurs, flowering-size bulbs fail to form a flower, which is a unique phenomenon for large-flower bulbs. There is a similar physiological disorder in certain cultivars of tulip cultivars.

Bacterial Diseases. There are two major bacterial diseases of bulbs, *Pectobacterium* (former *Erwinia*) *carotovora* subsp. *carotovora* and *Xanthomonas hyacinthi*. It is essential to prevent infections by best management practices, since chemical control is usually not very effective. Hyacinths and *Zantedeschia* (calla lilies) are highly susceptible to bacterial diseases (Van Aartrijk 1995).

Fungal Diseases. At least 26 genera of fungi affect flower bulbs (Byther and Chastagner 1993). Some are aerial while others are soil-borne. In addition, some are more prevalent in the field while others are more prevalent under greenhouse conditions. Thus, different control procedures must be utilized for each disease and growing environment. Major fungal diseases (most of which have specific species affecting different bulbs) are: *Botrytis* spp.; *Fusarium oxysporum* spp., the root-rot

complex of lilies; *Penicillium* spp.; *Phytophthora* spp.; *Rhizoctonia tuliparum* (“Kwadegrond”); *Stagonosporopsis curtisii*; *Stromatinia gladioli*; and *Trichoderma viride* of tulips. Of these diseases, *Fusarium* bulb rot of tulips causes not only the loss of the bulb; the infected bulb also produces ethylene, which causes many physiological disorders including flower abortion (Kamerbeek and De Munk 1976).

Nematodes. These parasitic organisms were partly responsible for the establishment of the BKD (see Section V.C.1) and the cooperative pre-inspection program of the USDA/APHIS (see Section V.C.8). They can occur in aerial parts (stems and leaves), bulbs, and roots. Most often, they have been controlled through the use of clean stock, tissue culture, HWT, and fumigation. Recently, fumigation has been affected by the restricted use of methylbromide, which is prohibited in most countries due to human health risks.

Viruses. At least 40 different viruses of varying types have been identified in ornamental geophytes (Bergman 1983; Byther and Chastagner 1993). Control can be achieved by tissue culture and roguing. In addition, insect vectors (e.g., aphids, thrips, and nematodes) can transmit viruses and must be controlled. The symptoms of many flower bulbs viruses are illustrated in the publications of Bergman (1983) and Van Aartrijk (1995).

3. Insects of Ornamental Geophytes. Baker (1993) provided a highly comprehensive review of the large number of insects that can affect flower bulbs. Examples of the major ones are: aphids and thrips (which can also be vectors of viruses); the lily beetle (small and large bulb flies that affect most species of *Amaryllidaceae*), bulb mites, fungus gnats, mealy bugs, and white flies.

4. Physiological Disorders of Ornamental Geophytes. Many flower bulbs are susceptible to physiological disorders, which are usually cultivar specific. Most are produced by low and/or high temperature stresses and/or nutrient deficiencies (De Hertogh and Le Nard 1993e). Some major examples are stem topple of tulips, flower abortion, abscission, and blindness in lilies, hyacinths, and tulips; floral stalk fasciations in *Narcissi*; and interrupted inflorescence development in *Liatris spicata*. Three disorders of the geophytic organ include:

1. Chalking in tulips and *Zantedeschia* (calla lilies), which can be caused by mechanical damage

2. Temperature-induced problems, such as heating in transit, which can cause flower abortion or total bulb loss in tulips
3. Freezing injury of lilies, which can produce flower abnormalities or total bulb loss

As indicated previously, ethylene is produced by *Fusarium*-infected tulips and can cause flower abortion (Kamerbeek and De Munk 1976).

5. Exogenous Plant Growth Regulators (PGR). Zimmerman et al. (1931) showed that exogenous ethylene causes many physiological disorders on several flower bulbs plants. However, it is only since the early 1970s that many other exogenous PGR have become available for commercial use on flower bulbs. Instructions for the use of many of the PGRs are changed yearly and are available on Web sites (North Carolina Agricultural Chemicals Manual 2008). In addition, most chemical companies publish technical bulletins that contain specific use information on their products. A range of physiological processes can be influenced by PGR, including: the control of flowering in Dutch irises; control of leaf yellowing in lilies; control of marketable plant heights of daffodils, tulips, and lilies; and propagation by tissue culture or stem cuttings. There are many methods to apply the PGR (Barrett 1999). The system and PGR used depends on species and/or cultivar, bulb size, and the desired physiological response (Table 1.9).

D. Other Research Areas

1. Specialized Facilities and Equipment for Flower Bulbs. Due to the unique horticultural features and requirements of ornamental geophytes, many specialized growing, handling, treating, and storage facilities and equipment have been developed. In this review, however, only a few key examples are cited. The development of the specific facilities are dictated by the marketing objectives—for example, whether the bulbs are intended for regular (short-term) storage and subsequent domestic usage or export or whether they are being held for long-term storage. Five examples of bulbs being held for long-term storage are:

1. Bulbs being held for shipment to the southern hemisphere (Blaauw et al. 1930; Beijer and Van Slogteren 1933; Beijer 1938, 1948)
2. Bulbs being forced as Eskimo or frozen tulips for fall flowering (De Jong et al. 1991; De Jong and Buurman 1992; De Hertogh 1996)
3. Retardation of Dutch *Iris* for year-round flowering
4. Delaying flower initiation of immature tulip bulbs (Le Nard 1975)

Table 1.9. Examples of the effects of exogenous plant growth regulators on the growth and development and flowering of ornamental flowering bulbs.

Growth regulator	Application method	Plant response	Reference
Ancymidol	Dip, drench, spray	Reduced marketable plant heights, of Anemones, Dahlias, freesias, and tulips	De Hertogh 1996
Auxins and cytokinins		Increase in number of propagules	Kim and De Hertogh 1997
Daminozide	In culture medium Spray	Reduced marketable heights of Anemones and <i>Ranunculus</i>	De Hertogh 1996
Ethanol	Rooting solution	Reduced scape and leaf growth of forced Paperwhite Narcissi	Miller and Finan 2006
Ethephon	Spray	Reduced scape and leaf growth of daffodils and hyacinths	De Hertogh 1996
Ethylene	Gas	Induction of flowering in Dutch Irises	De Munk and Schipper 1993
Gibberellins	Dip	Floral abortion of lilies and tulips Increased number flowers of <i>Zantedeschia</i>	Hitchcock et al. 1932 Funnell 1993
Flurprimadol	Spray Dip, drench	Inhibiting leaf yellowing of <i>Alstroemeria</i> and lilies Reduced marketable heights of daffodils, hyacinths, lilies, and tulips	Hicklenton 1991; Ranwala and Miller 1998 Krug et al. 2005a,b, 2006a,b
Jasmonic acid	Paste	Gummosis of tulip bulbs	Saniewski 1989
1-MCP	Gas	Extended vase life of cut flowers	Blankenship and Dole 2003
Paclobutrazol	Dip, drench	Reduced marketable heights of freesias and tulips	De Hertogh 1996
Uniconazole	Dip, drench, spray	Reduced marketable height of lilies	De Hertogh 1996

5. Modified atmosphere storage (ultra-low-oxygen [ULO]) of lilies and tulips for long-term storage.

Special facilities are also required for the control of the *Narcissus* bulb fly and nematodes (Lane 1984; Byther and Chastagner 1993). Also, Courtney et al. (1947), Woodville (1971), and Lane (1984) have provided plans for the construction of hot water treatment (HWT) tanks. ULO storage systems have been developed to retard the development of lilies and tulips in order to maintain flower quality when forced. A patented method has been developed to control the humidity in the planting cells and in combination with a controlled temperature regime; it is not necessary to seal the crates of planted tulips. This method prevents the dehydration of the tulip shoot (Wildenbeest 2007). Also, high-temperature retarding storage facilities have been developed for Dutch Irises (De Munk and Schipper 1993) and freesias (Imanishi 1993). The effects of low-pressure storage (LPS) was studied on four bulbs species by De Hertogh et al. (1978), but the system did not demonstrate commercial possibilities.

2. Transportation of Flower Bulbs. Depending on the distance and presence or absence of water barriers, flower bulbs can be transported to other countries by truck, air, or ship. For successful bulb transport, eight special factors must be considered:

1. Type of packing materials
2. Temperature and storage conditions after lifting and prior to shipping
3. Temperatures during shipping
4. Ventilation requirements of the bulbs
5. Relative humidity requirements
6. Duration of the transport period
7. State of dormancy during the shipping period
8. Effects of ethylene on the shipped species

Until the late 1960s and early 1970s, most bulbs shipped to the United States and Canada from the Netherlands generally were packed in paper bags with small holes for ventilation and placed in wooden crates on pallets. On the ship, they were placed under the water line to keep them cool. This method of shipping changed significantly with the advent of the controlled temperature containers (reefers) in the early 1970s. Concurrently, bulbs requiring excellent ventilation were packed in

stackable plastic trays. Later generations of reefers control the relative humidity, which assists in controlling diseases and premature rooting during transport. Beginning in the late 20th century, the Sprenger Instituut in Wageningen, the Netherlands, was responsible for certifying the containers that carried flower bulbs. In addition to the reefers, the use of temperature recorders began in the late 1960s. Currently, recorders also monitor relative humidity levels during transport.

3. Forcing and Greenhouse Technology. To properly program flower bulbs for forcing, controlled temperature facilities are needed. For the forcing of spring flower bulbs, rooting rooms have been developed (De Hertogh 1996; Van Nes 1988). These facilities are used in conjunction with the cold weeks required by these bulbs and often utilize moving benches to reduce labor inputs. For the hydroponic forcing of tulips, which has increased in recent times, rooting rooms and benches have been modified to accommodate this medium. In addition, as the worldwide forcing of lilies has increased, freezers have been constructed to hold the bulbs at -1°C to 2°C .

The climatic control of the greenhouse environment is very important for the forcing of flower bulbs. Proper climate control assists in eliminating or minimizing the incidence of diseases, insects, and physiological disorders, such as flower abortion. Also, the marketable quality of the potted plants and fresh-cut flowers can be enhanced which can increase profitability (De Vroomen 1993). The global forcing industry is fortunate that it has access to many publications (Materlerz 1977; Hanan et al. 1978; Langhans 1990; Aldrich and Bartok 1994; Van Doesburg et al. 1999; Bartok 2001; Nelson 2003; Kamp and Timmerman 2002) that have focused on the greenhouse environment. In addition, many commercial companies have specialized in developing this equipment; they advertise in trade papers and on the Web, and exhibit at trade shows, such as the Horti-Fair in Amsterdam and the OFA Short Course in Columbus, Ohio.

V. MAJOR FLOWER BULB ORGANIZATIONS

A. Commercial, Semigovernmental, and Governmental Agencies

1. AGREXCO. The Israel's leading agricultural exporter, also called Carmel (www.agrexco.co.il/en/home.asp), was founded in 1956. In addition, more than 60 flower export companies are registered in Israel (www.moag.gov.il/news/flow.htm). AGREXCO is owned jointly by the

government of Israel and the growers of all horticultural products. The company has four aims:

1. Develop a worldwide marketing strategy for the Israeli-grown agricultural products.
2. Develop air, sea, and land logistics and transportation networks.
3. Offer a range of products by developing new cultivars and upgrading existing ones.
4. Ensure that product quality meets international standards.

AGREXCO has a board of directors (the current chairman is Mr. Y. Tsur) and a managing director (currently, Mr. S. Tirosh). The AGREXCO marketing network consists of 9 sales centers, 8 in Europe and 1 in the United States, and 2 merchandising centers in Israel. It supports research in coordination with the Volcani Center (Agricultural Research Organization) of the Ministry of Agriculture, the Hebrew University, and several integrated regional research units. These joint efforts have produced new cultivars of Paperwhite *Narcissus* and *Hippeastrum* and forcing protocols for numerous ornamental geophytes, such as Paperwhite *Narcissus*, *Leucojum aestivum*, *Ornithogalum dubium* (De Hertogh 1996; Kamenetsky 2005; Sandler-Ziv et al. 2008; Cohen et al. 2008). Experiments on propagating materials and fresh-cut flowers have produced a database for the optimal temperatures, humidity, and ventilation rates for all postharvest phases (Philosoph-Hadas et al. 1997, 1999, 2000). These developments have not only maximized the shelf life of the products but also extended their worldwide marketing season.

2. ANTHOS (BGBB/BOND). The Dutch Bulb Exporters Association (BOND) was founded in February 1900 (Krelage 1946; Bot and Hooftman 2000). In 1995, the BOND merged with Holland Plant Exporter Association and the name was changed to the BGBB. ANTHOS, the organization's current name, celebrated 100 years on February 10, 2000. It has an executive director (currently, Mr. H. Westerhof), and a secretarial and accounting staff. The executive director reports to a general board of directors. In addition, the export of flower bulbs is divided into 5 country groups, and each has a board of directors. In 1900, there were 7 export groups, but later it was increased to 10. Now there are 5. These changes in the number and composition of the groups reflect the changing global markets. North America and Canada is Group I and is the oldest group; it has been a leader in the support of many exporter-related needs. One primary function of Group I is to coordinate and fund

the USDA/APHIS and Canadian Agricultural Inspection for the Pre-shipping Bulb Inspection System. This system was developed in 1950 and revised in 2006 (PD 2006) to prevent the entry of soil and pests that are specified in the USDA/APHIS Plant Quarantine, regulations Q-37 (USDA/APHIS 2008). In addition, Group I has supported research in North America, which contributed significantly toward the publication of *Holland Bulb Forcer's Guide* (De Hertogh 1996) and *The Physiology of Flower Bulbs* (De Hertogh and Le Nard 1993). Currently, the group supports research directed by Dr. W. B. Miller at Cornell University, Ithaca, NY.

3. Flower Bulb Auction Houses. There are two types of flower bulb auction houses in the Netherlands (see Sections V.4 and V.5). In addition, traditionally, there have been two types of bulb auctions: the field auction of specific bulb crops and cultivars and the dry bulb auction. In the field auction, the grower offers the crop to the auction house, which then is sold at a green stage. The buyers, mostly bulb growers (Kwekers), have an opportunity to inspect the crop prior to the official auction, which uses oral bidding. Krelage (1946) reported that the first field auction was held in 1657 at Leyden.

Up to 2006, the auction houses had dry auctions. Growers sent their clean, dry, and properly sized bulbs to either the CNB or HOBACHO (described in the next sections) in Lisse. Both houses used auction clocks, and bulbs were sold to growers and exporters. In September-October, the auction houses also had planting stock auctions, which were included in dry sales. The first dry auction was also held in Leyden, in 1666 (Krelage 1946).

In 2006, the CNB and HOBACHO auctions terminated their dry auctions; thus, bulb prices are no longer based on the auction clock system. Currently, prices are controlled by production statistics, weather conditions during the growing season, and, of course, exporters' projected sales. Representatives of the auction houses who are familiar with these factors act on behalf of growers and exporters.

4. Coöperatieve Nederlandse Bloembollencentrale (CNB). The Coöperatieve Nederlandse Bloembollencentrale (CNB) was founded in 1975 by merging two bulb cooperative auction houses, the West Friesland in Bovenkarspel, founded in 1919, and the Hollandsche Bloembollenkweekers Genootschap (HBG) in Lisse, which was founded in 1924. Most of the bulbs in the Bulb District, the region between Haarlem and Den Haag (The Hague), are grown on sand and are exported to the United States. In contrast, in the Bovenkarspel region, most bulbs are grown on

clay, and a mixture of both clay- and sand-grown bulbs is used domestically and for export to the other countries. Both cooperatives have controlled-temperature storage facilities to provide the temperature and other treatments for a wide range of flower bulbs. The facilities in Bovenkarspel also can provide ULO storage. In addition, the CNB has representatives in all flower bulb-growing areas in the Netherlands. They coordinate the bulb transactions between the exporters and growers.

5. Holland's Bloembollenhuis (HOBACHO). The Holland's Bloembollenhuis (HOBACHO) was founded in Lisse, the Netherlands, in 1920 as a private company. The founders were L.J. Homan, H. Bader and D. Hogewoning Hz. (Zwetsloot 1996). The auction house used the first two letters of the last name of each founder and has become well known as the HOBACHO. Up until a few years ago, the HOBACHO held both field and dry auctions. Like the CNB, the HOBACHO has representatives in all bulb-growing areas. It has controlled storage facilities in Hillegom and Heemskerk. In 1988, the Testcentrum voor Siergewassen (Test Center for Ornamental Plants) was founded by the HOBACHO. The objective was to cover the entire production chain from the hybridization to the sale of the flowers. Since its founding, the hybridization of tulips, hyacinths, and lilies has been carried out, as well as studies on the physiology of some bulbous crops from Israel and South Africa. The hybridization studies have focused on disease resistance, polyploidy, flower colors and shapes, keeping quality, and the ability to be forced worldwide.

In 1999, the HOBACHO became a subsidiary of the Flower Auction Aalsmeer (VBA), which is currently called Flora Holland. Thus, it is no longer a private company.

6. HBVeilingen. After termination of the dry sale auctions by the CNB and HOBACHO, a new private auction house, HBVeilingen, was founded in 't Zand, the Netherlands, in 2006, by Henk Hoogervorst. This auction has flower bulb warehouses in two locations. Their auction system is as follows:

1. Before 1200 hours (noon), the bulbs must be in one of the two warehouses.
2. After 1400 hours (2 pm), a catalog with the crop, cultivars, and other information is published and also placed on the Internet (www.hbveilingen.nl).
3. Between 1400 and 0800 hours (8 am) of the next day, bids are submitted by buyers.

4. At 0800 hours (8 am), the auction starts and a buyer can bid on the whole or part of the lot. If only a part is bought, the next highest bidder can have the remainder of the lot.
5. The bulbs are delivered to the buyer later in the day. Because prices are dependent on supply and demand, it is expected that this will be the future system for the purchase of bulbs in the Netherlands.

7. Dutch Promotion Organizations (CBC/Raad/IBC). The Central Flower Bulb Committee (CBC) was organized on July 10, 1925 in Haarlem, the Netherlands (Franken 1931). In 1968, all offices and facilities were moved to Hillegom. It has also been called the Associated Bulb Growers of Holland and the Flower Bulb Council (Raad voor Bloembollenondernemers). However, since 1986, it has been called the International Bulb Centre (IBC). Worldwide, the IBC has several responsibilities:

- Market research
- Public relations
- Advertising
- Providing technical advice and product information
- Participating in flower exhibitions (see Section V.C)
- Providing promotional and educational materials and information
- Providing visual services

It has branch offices in several countries, with one in the United States. Funding for the IBC is supplied the Dutch bulb growers and related trade organizations. It maintains a Web site (www.bulbsonline.org) describing its products and services.

In the United States and Canada, the International Flower Bulb Information Center (IFDIC) carries out the functions of the IBC. The predecessor of IFDIC, the Netherlands Flower Bulb Institute (NFI), was established after World War II under the direction of Margaret Herbst. She was replaced by Gustave Springer, who served as the director from late 1940s until his retirement in 1981. He was the industry liaison for the flower bulb research program that was established initially at Michigan State University (MSU) and later at North Carolina State University (NCSU) under supervision of Dr. A. A. De Hertogh. Tim King and Robert LaRue served as directors of IFDIC before the office was closed about 1985. There was a similar office in the United Kingdom called the Bulb Information Desk, and Frederic Doerflinger (Doerflinger 1973) was the director.

8. Royal General Bulbgrowers' Association (KAVB). The Royal General Bulbgrowers' Association (KAVB) was established on June 1, 1860 (Franken 1931; Krelage 1946). At the time, the major goal was to organize flower shows to promote the sale of flower bulbs (see Section V.C). Initially, the members of the KAVB were primarily flower bulb exporters and traders. Subsequently, the KAVB became a bulb growers' organization, but exporters are still members. It has a board of directors with a chairman (currently, Ir. J.J.J. Langeslag), a managing director (currently, Dr. J. van Aartrijk), and several committees and bulb societies. The KAVB has four major functions:

1. It is active in political and economic areas that affect the interests of its members, such as fertilizers and environmental issues related to water quality. To accomplish this, the KAVB supports the administrative activities of several societies for products, such as dahlias, hyacinths, lilies, narcissi, and tulips. It is divided into regions or cities.
2. It provides a service to settle disputes between buyers and sellers through its bulb arbitration board.
3. It is responsible for the national and international registration of almost all commercially produced flower bulbs. The major exceptions are daffodils (Kington 1998) and lilies (Matthews 2007), which are registered by the Royal Horticultural Society in the United Kingdom. The KAVB regularly publishes official classified lists on tulips, hyacinths, and specialty bulbs. In addition, this committee oversees the weekly flower shows that are held for the industry in Lisse.
4. In the past, the KAVB published the weekly trade periodical "*Weekblad voor Bloembollencultuur*," which contained many scientific and popular articles written for the industry. This information is currently published by the CNB in *BloembollenVisie*. The KAVB maintains a Web site (www.kavb.nl) and publishes an annual report for its members. It also maintains the most extensive library for flower bulb literature in the world. Drs. Johan van Scheepen is the curator (vanscheepen@kavb.nl).

9. Produktschap Tuinbouw (PVS/PT). The Produktschap Tuinbouw (PT, Horticultural Marketing Board) is the successor of the Ornamental Marketing Board of The Hague (PVS). It has a board of directors with representatives of the five horticultural branches—flowers and pot plants, flower bulbs, trees, vegetables and fruit, landscape and gardens—as well as representatives of the energy and economy

committees. Each PT committee has a board in which the trade unions are also members. Members of the flower bulb committee include the KAVB, ANTHOS, bulb auctions, bulb wholesalers, PLANTUM (an association for breeders, tissue culture, production of seed and young plants), and the trade unions. The board of each committee is completely independent. They decide which levies (marketing taxes) are acceptable and how the funds are to be spent. In 2006, the Flower Bulb Committee appropriated 41% of its income for promotion and marketing and approximately 12% for research (Produktschap Tuinbouw 2007).

The income of the flower bulb committee is related to each flower bulb transaction. Every bulb grower, exporter, wholesaler, and retailer must pay a specified percentage of each financial transaction. Since most bulbs are sold through commissionaires that are employed by the bulb auctions, they deduct the funds for the PT after the sale has occurred. The buyer must pay an additional amount. Thus, the bulb auctions pay directly to PT. Growers who force their own bulbs pay a percentage of the sales to the PT. Finally, the grower must pay for the planting stock, based on a financial survey of the stock. Thus, the yearly income of the flower bulb committee of the PT is variable; consequently, the amount of money available for research and the IBC functions varies annually.

10. North American Flowerbulb Wholesalers Association (NAFWA).

The North American Flowerbulb Wholesalers Association (NAFWA) was organized in Chicago, Illinois in 1983 and is still active (www.nafwa.com). In January 1984, at its annual meeting in Chicago, it merged with the Horticultural Dealers Association, which was formed in 1975. The objective of the merger was to have one major flower bulb organization to establish common policies and goals. NAFWA is comprised of two types of members, full and associate. Full members (normally 20–25) are the North American–based flower bulb importers and wholesalers. Associate members (normally 25–30) are allied organizations that either produce and/or export flower bulbs or are associated with essential flower bulb needs, such as shipping. NAFWA has four objectives:

1. To establish, communicate, and support the marketing and research needs of North America
2. To promote educational scholarships and programs, for example, Bulbs for Children
3. To evaluate transportation issues for sea and air shipments
4. To assist with the flower bulb inspection programs associated with the USDA/APHIS and Homeland Security
5. To promote and distribute research and marketing information

NAFWA cooperates with ANTHOS and the IBC of the Netherlands and other global organizations, such as AGREXCO of Israel and HADECO of South Africa. NAFWA also has a representative on the Research Committee of Group I of ANTHOS. Traditionally, this committee has advised flower bulb researchers at U.S. land-grant universities (e.g., Michigan State University, North Carolina State University, and Cornell University) on the industry's perceived research needs. It has have been an essential group in making North America the largest market for flower bulbs outside of the Netherlands (Table 1.2).

B. Research and Technical Support Organizations by Countries

1. The Netherlands Bloembollenkeuringsdienst (BKD). The Bloembollenkeuringsdienst (BKD) and the Dutch Plant Protection Service (PD) were established in 1923 to inspect flower bulbs (Van Os 1971; Veenenbos 1971). The first 75 years of the BKD has been documented by Meertens (1998). Professor Van Slogteren of the LBO and the KAVB was instrumental in establishing these service organizations. Field inspections for pests such as the *Narcissus* bulb fly (*Merodon equestris*) and the nematode, *Ditylenchus dipsaci*, were initiated in the early 1920s. The bulb fly led to an embargo of Narcissi to the United States, and, therefore, the BKD was formed. In 1937, compulsory bulb inspections were mandated by the United States. Since its inception, the BKD has had five directors: Mr. W. van der Laan (1923–1935); Mr. F. Limburg (1935–1963); Ir. H. van Os (1963–1994); Ir. C. Maenhout (1994–2007); and Mr. J. Goebbels who was appointed in March 2007. The BKD is responsible for ensuring bulb quality and has over 60 inspectors. In 1982, the BKD moved into its current facilities, which were updated in 1998/99. The facilities consist of offices for the director, staff, and some of the inspectors; laboratories; greenhouses; and outdoor testing fields. The BKD maintains a Web site (www.bloembollenkeuringsdienst.nl) describing its services.

The Laboratorium voor Bloembollen Onderzoek (LBO/BRC/PPO). Like the BKD, the origin of the Laboratorium voor Bloembollen Onderzoek (LBO) is related to two major diseases of flower bulbs: the yellow disease of hyacinths, which can be found not only in the field but also in dry storage and is caused by the bacterium *Xanthomonas hyacinthi* (Wakker 1883, 1884, 1885), and the nematode in Narcissi. This disease had been identified at the beginning of the 20th century. Research showed a decrease in yield due to the nematode infections. Because of

the large number of programs that were conducted by the LBO's more than 20 scientists and 80 coworkers, several major research areas will be covered here.

In addition to the research on the yellow disease on hyacinths by Wakker (1883, 1884, 1885), Smith (1901) described the ecology of the bacterium and precisely described the symptoms. Nematodes were identified in *Narcissi* early in the 20th century. Research showed that they cause a decrease in yield. As a result of these two disease problems, Dr. E. Van Slogteren was appointed in 1917 as the "phytopathologist for the Bulb District" at Lisse, the Netherlands. Van Slogteren (1918, 1920, 1923) showed that the solution for the nematodes in *Narcissi* and hyacinths was a hot water treatment (HWT). In contrast, solutions for the yellow disease took longer to discover.

From 1920 to 1922, the LBO facilities were constructed next to the Horticultural College in Lisse. In, 1925 the LBO became an institute of the Landbouwhoogeschool (currently, the Wageningen University and Research). The official name of the laboratory was Institute for Phytopathology with the subtitle Laboratory for Bulb Research. Dr. Van Slogteren was appointed as extraordinary professor of the Phytopathological Department in Wageningen.

In the 1920s, physiological research was started on a disorder called toppling of tulips. Pinkhof (1929a,b) investigated the cause and the conditions that promoted the disorder and focused on carbohydrate levels in the bulb. Uyldert (1934), who was not employed at the LBO, studied the uptake of various salt solutions. Later, Algera (1968) concluded that calcium deficiency was the cause because of slow uptake and mobilization or transport of the minerals. Also, during this period, Beijer (Beijer 1929; Beijer and Van Slogteren 1930; Beijer 1936) conducted research on storage temperature treatments for early forcing and for the transport of bulbs to the southern hemisphere (Beijer 1938, 1955). Temperature treatments for nonplanted bulbs have continued to be an important area of research for all bulbous crops (see Proceedings of the ISHS International Symposia on Flower Bulbs, Bergman et al. 1971; Rees and Van der Borg 1975; Rasmussen 1980; Bogers and Bergman 1986; Doss et al. 1990; Saniewski et al. 1992; Lilien-Kipnis et al. 1997; Littlejohn et al. 2002; Okubo et al. 2005; Van den Ende and Gude 2009, in press).

In 1972, Beijer summarized the literature and symptoms of the yellow disease of hyacinths, including the infection, development of the disease in the leaves, and transmission to the bulbs. He also described inoculation experiments under field conditions. Currently,

more than 100 years after the first publication by Wakker in 1883, research is still being conducted on the characterization, detection, and control of yellow disease (Van Doorn 2002).

The phenomenon of tulipmania (1636–1637) in the Netherlands is well known (Krelage 1942; Blunt 1950; Goldgar 2007) and beautifully illustrated (Segal 1998). It has been said that during this period, there was a dialogue between two tulip growers, Mr. Waermond and Mr. Gaergoedt (cited by Van Damme 1900). While discussing bulb prices, Mr. Gaergoedt described a method to obtain broken tulip flowers by cutting two tulip bulbs, one of which had a broken flower and the other that was not broken. By tying the two halves, a tulip with a broken flower was produced. At that time, it was not known that broken tulips were virus infected. Later, Van Slogteren and De Bruyn Ouboter (1941b) conducted an experiment, based on this dialogue, and the results were in agreement with the report from 17th century.

The LBO has conducted virology research not only on bulbous crops but also on potatoes and sugar beets. Initially, it was one of the facilities in the Netherlands to produce antisera for these crops (Van Slogteren 1943). Van Slogteren and De Bruyn Ouboter 1941a,b; 1946 investigated viruses in Narcissi and tulips. They described the symptoms (illustrated in color), transmission of the viruses, spreading under normal conditions, and finding the most economic methods to control them. Later, the diseases were diagnosed by electron microscopy (De Bruyn Ouboter et al. 1951). Virology research also focused on serological methods to obtain virus-free stocks and on virus diagnostics (Van Slogteren 1955).

In the 1930s, studies were conducted on the respiration of hyacinths and tulips as a part of the research on the yellow disease and changes in carbohydrates in tulips that were influenced by temperature treatments (Dolk and Van Slogteren 1930; Algera 1936, 1947). Other physiological research was initiated in the 1950s. Kamerbeek (1958) investigated the blueing of tulips and demonstrated that it was a physiological disorder. Subsequently, Kamerbeek (1962) studied the respiration of bulbous *Iris* and the influence of temperature on the differentiation of the apical primordia, especially the twijfelmaten (the minimal bulb size for flowering). In addition, Beijerbergen (1969) isolated and investigated a precursor of α -methylene-butylolactone, called tulipalin. It was present in the white, fleshy scales of the tulip, and he concluded that it played a role in the resistance against the infection by *Fusarium oxysporum* f. *tulipae*. The bulb, however, becomes susceptible when the dry tunic is formed and there is a subsequent decrease in concentration of tulipalin.

In tulips, flower bud necrosis can be caused by various storage conditions. De Munk (1971, 1972, 1973) and De Munk and Beijer (1971) found that ethylene is a major factor in inducing this physiological disorder. Later, Kamerbeek and De Munk (1976) reviewed the effects of ethylene on a wide range of bulbous crops.

Prior to 1963, research at the LBO focused on the biology and control of pests and the influence of temperature and diseases on the flowering of bulbous crops. After 1963, the research goals were changed to include applied studies that closely supported the needs of the bulb industry (e.g., bulb growth and production, temperature treatments, mechanization, and profitability). Thus, a new department was formed with specialists for each major crop and one for the specialty bulbs (previously called minor or miscellaneous bulbs). In addition, other Dutch governmental institutes stationed researchers at the LBO.

From 1917 to 1973, the LBO was a part of the Landbouwhogeschool in Wageningen. In 1973, the LBO officially became the Experimental Station for Bulbous Crops and was no longer an institute of Wageningen University. In 2001, the name was changed to Praktijkonderzoek Plant en Omgeving–Bollen en Bomen (PPO Bulbs and Trees). Currently, the PPO is a part of the Wageningen University and Research. Thus, the affiliation has gone full circle.

Sprenger Institute. In the 1970s, the Sprenger Institute at Wageningen became involved in bulb research. The primary research areas were:

- Keeping quality of bulb flowers, such as Dutch *Iris* (Staden and Van den Berg 1977) and Narcissi (Boer and Harkema 1978)
- The effects of adding flower preservatives the water (Staden and Sloodman 1977; Staden et al. 1978)
- The storage of bulbs
- Optimal conditions for the transport of bulbs (Verbeek 1980)

In 1965, Hering published a report with photographs of bulb packing materials and their condition on arrival in the United States. In the 1970s, bulbs began to be packed and shipped in containers. The first type was the clip-on containers (Meffert and De Pagter 1972; Yekutieli and Van Nieuwenhuizen 1974a,b). When temperature-controlled containers became available for transporting bulbs, the Sprenger Institute became the institute for their inspection and certification (Van Nieuwenhuizen 1981).

Temperature during storage of nonplanted bulbs in the old warehouses was controlled either by heating pipes or opening the doors

in the outer walls. Subsequently, storage warehouse with many cells were constructed with temperature and ventilation control systems. Thus, energy became an important economic factor (De Vroomen 1993). Since each crop has its own temperature requirements, energy use was studied for tulips (Boerrigter and Bouman 1982) and hyacinths (Boerrigter and Bouman 1984). Also ethylene and carbon dioxide was measured in the ventilation air during the preparation treatments of hyacinths (Boerrigter and Bouman 1983).

Agricultural University Wageningen. Starting in the 1920s, bulb research on florogenesis and physiology was conducted by Professor A. Blaauw and his coworkers in the Department of Plant Physiology (see Section IV). In addition, the Department of Horticulture investigated many bulbous crops. Some of the research projects were:

- Shortening the juvenile phase in tulips (Fortanier 1971, 1973)
- The influence of temperature and light on *Brodiaea* (Fortanier 1969), Dutch *Iris hollandica* (Fortanier and Zevenbergen 1973), and *Nerine* (Van Brenk and Benschop 1993)
- Dormancy and sprouting in *Gladiolus* (Apte 1962)
- The influence of ethylene and smoke on the release of dormancy in *Freesia* (Imanishi and Fortanier 1982a) and Dutch iris (Imanishi and Fortanier 1982b)

The effects of plant growth regulators were also studied. Some of the areas were:

- Possibilities for commercial use in tulips (Van Bragt and Van Gelder 1979, 1982)
- Effects on flower formation (Van Bragt et al. 1986)
- Year-round flowering of *Eucharis amazonica* (Van Bragt and Sprenkels 1983)

Bulb Research at Other Dutch Universities. Recently, physiological research on bulbous crops has been transferred from Wageningen University to the universities of Utrecht (Dr. Kollöfel) and Amsterdam (Dr. Van der Plas) and then returned to Wageningen (Dr. Van der Plas). The effects of low temperature requirements on tulips were investigated. It was demonstrated that growth and flowering (Lambrechts 1993), respiration (Kannevorff 1995), gibberellin responses (Rebers 1994), membrane lipids (Walch and Van Hasselt 1991;

Walch 1997), and the sensing low temperatures (Rietveld et al. 2000) were significantly influenced by temperature.

Instituut voor de Veredeling van Tuinbouwgewassen (IVT). The Instituut voor de Veredeling van Tuinbouwgewassen (IVT) was founded in 1943 and initially covered all aspects of breeding horticultural crops except flower bulbs (Lodewijk 1985). Due to governmental statutes, flower bulb breeding supposed to be a part of the research program of the LBO but was never developed there. In the meantime, breeding was carried out exclusively by the flower bulb industry and not scientifically. Subsequently, the IVT started flower bulb breeding research in the 1960s in order to provide a scientific basis for breeding of flower bulbs. Initially, Zeilinga and Schouten (1968a,b) published a list of chromosome numbers in tulips and methods to obtain tetraploidy. Later, Ir. J. P. van Eijk and his assistant W. Eikelboom were joined by Dr. J. M. van Tuyl. They conducted research on the breeding of tulips, hyacinths, Dutch iris, and gladioli. Their efforts focused on disease resistance, development of testing systems, earliness, self-incompatibility, polyploidy, color, breeding techniques, tissue culture, and so on (see Section IV.B.4, 5, 6, 8). In 1992, the hyacinth breeding project terminated and Dr. Van Tuyl initiated his lily research, which is still being conducted.

Plant Research International (PRI). When IVT became the CPRO-DLO and, subsequently, the PRI, flower bulb projects were focused on the tulip, lily, and *Zantedeschia*. Tulip research was conducted on interspecific hybridization (Van Creij 1997) and ovary-slice culture and ovule culture and medium composition (Van Creij et al. 1999, 2000; Van Tuyl and Van Creij 2006). *Erwinia*, which is often the main cause of reductions in flowers and tuber yield of *Zantedeschia*, was investigated, and it was found that the resistance level is based on plastome-genome incompatibilities (Snijder 2004; Snijder et al. 2004). The lily breeding research is concentrated in two areas: (1) introgression breeding through use of sexual polyploids of hybrids between *Lilium longiflorum* × Asiatic hybrid lilies; and (2) introgression breeding studies on Oriental hybrids × Asiatic hybrid lilies. Introgression breeding can introduce a restricted number of traits from the donor species to the recipient. Traits can include flower color, disease resistance, flower shape, and forcing ability (Lim and Van Tuyl 2006). The lily research group has a Web site (www.liliumbreeding.nl), which provides information on the projects and publications by the group. It also links to the Web sites of commercial lily breeders of the Netherlands, many of which sponsor the lily breeding research at PRI.

Van den Hoek Foundation (Stichting). In the winter of 1939–1940, Frans A. van den Hoek, 't-Veld, Oude Niedorp, the Netherlands, was asked to force tulips for a local flower show; this was the beginning of his company. In 1968, Van den Hoek and Jonkheer published a list of tulip cultivars that could be used for the different flowering periods using precooled and nonprecooled bulbs. His son, Jan, has been a technical advisor to the Dutch-sponsored research programs at Michigan State University (MSU), North Carolina State University, and Cornell University. At MSU, Dr. A. A. De Hertogh and Jan van den Hoek developed the system of using the number of cold-weeks for many of the spring-flowering bulbs. They were divided into the use of minimum, optimal, and maximal number of cold-weeks, which is dependent on the bulb-growing season. This system was also used in the Van den Hoek forcing database. In 1981, the Van den Hoek Company became a foundation. In 1991, a database was published for both the benefactors of the foundation and for the bulb industry. Every year, an addendum is published. Thus, data for more than 1,400 tulip cultivars are available on a CD.

Van den Hoek developed forcing programs for the various flower shows that are open to the public (see Section V.C); the weekly show of the KAVB is open only to the industry. Since July 2007, the Van den Hoek Broeiproevenbedrijf (Flower Bulb Forcing Company) is a part of the trial and experimental garden in Zwaagdijk-Oost, the Netherlands.

2. France. The Institut National de la Recherche Agronomique (INRA) is responsible for all research, including social and economic aspects, associated with agriculture, food, and the environment in France. Research on flower bulbs in INRA began about 1955. At that time, there was a significant level of bulb production of Gladioli, tulips, *Narcissus* (tazetta types), and to a lesser extent dahlias, anemones, *Ranunculus*, and *Zantedeschia aethiopica*. The southeast of France was becoming an important area the winter production of long-stemmed tulip flowers (the so-called French tulips) that were exported to various countries in the world.

Initially, research was devoted to the major pathological problems encountered with Gladioli (e.g., *Fusarium* and grassy top disease) and tulips (e.g., *Fusarium* and viruses) during bulb and flower production. This research was conducted in the Research Station of Antibes, mainly by Dr. R. Tramier, and, in Versailles, by Dr. Mrs. D. Grouet, Dr. Mrs. M. Lemattre, and Dr. Mrs. J. Albouy.

Research on the physiology of Gladioli, tulip, and bulbous *Iris* started in 1965 in the research station of Ploudaniel, which is located

in Brittany in the west of France. Dr. J. Cohat and Dr. M. Le Nard, the research leaders, investigated the relationship between bulbing and flowering of several ornamental geophytes. The objective was to enhance the knowledge of the physiological basis of these processes and thus allow growers to reduce the risks of problems during bulb and/or flower production. This was especially needed for out-of-season flower production. The major results of this research are summarized in De Hertogh and Le Nard (1993).

Plant breeding programs on flower bulbs were initiated in 1965 in Ploudaniel by Dr. J. Cohat for Gladioli and Dr. M. Le Nard for tulips and bulbous *Iris*. In about 1967, plant breeding programs for anemones and *Ranunculus* were initiated by Dr. J. Meynet in the Research Station of Fréjus located in the southeast of France. In addition to classical breeding approaches, in vitro techniques were also investigated. This program led to the release of new cultivars highly adapted to winter flower production in Mediterranean areas. It also contributed greatly to the improvement of the quality of the flowers. The new cultivars and technology have been adapted by many French companies.

The new tulip cultivars produced by the INRA breeding program have been, and still are, grown primarily by Dutch companies. Some of them are 'Alibi', 'Avenue', 'Fontainebleau', 'Pieter de Leur', 'Remise', 'Residence', and 'Silhouette Bouquet'. Due to the retirement of the researchers cited earlier and reduction of funds, research devoted to flower bulbs was discontinued between 1995 and 2005.

3. Israel. Ornamental geophytes are a major component of the ornamental industry in Israel. Being a significant center of ornamental horticulture in a warm-climate region, Israel has established programs for the development of flower crops suitable for these climatic conditions as well as new technologies for crop cultivation, breeding, storage, and transport to other countries.

The Hebrew University. The Faculty of Agricultural, Food, and Environmental Quality Sciences of the Hebrew University of Jerusalem was established in 1942 in Rehovot, as the Institute for Agricultural Sciences. During the past 60 years, ornamental crops were studied in two divisions of the faculty: the Department of Ornamental Horticulture and the Department of Agricultural Botany. In the early 1960s, research on flower bulbs was initiated by Dr. A. H. Halevy. The physiology of flowering and methods of flowering control were investigated by Drs. A. H. Halevy, N. Zieslin, R. Shilo, A. Borohov, and D. Weiss. They focused on the thermo- and photoperiodic induction of flowering

and the effects of auxins, gibberellins, cytokinins, and carbohydrates in *Brodiaea*, *Gladiolus*, *Ranunculus*, *Zantedeschia*, *Liatris*, and several other species. The six-volume *Handbook of Flowering*, edited by A. H. Halevy (1985–1989), is the most comprehensive treatise published on flowering. This series summarized the research on flowering of over 300 botanical species. The physiology of senescence and the postharvest physiology and handlings of flowers was conducted by Drs. A. H. Halevy and S. Mayak. They evaluated the physiological and molecular background of flower senescence, including the involvement of plant growth regulators, carbohydrates, and water supply. The development of new floriculture crops (e.g., *Agapanthus*, *Brodiaea*, *Leucojum*, *Nerine*, and *Iris*) for Israel was also investigated. The development of a new crop (see Section III.D) involves extensive research starting with the search for unique plant material, selection criteria, propagation, the control of growth and flowering up to the harvest stage, and marketing. Programs on in vitro propagation, storage organ formation, and flowering of geophytes have been conducted by Dr. M. Ziv.

Agricultural Research Organization (ARO), the Volcani Center. The founder of the Department of Ornamental Horticulture of Agricultural Research Organization (ARO) was Dr. E. A. Vega. He initiated research programs on ornamental geophytes and their production in early 1950s. Since the department's inception, Dr. Vega emphasized the importance of genetics and breeding of new cultivars for the development and advancement of the ornamental industry in Israel. The breeding programs were combined with physiological and agro-technical research and yielded many commercially important cultivars. The most famous are the Paperwhite *Narcissus* 'Ziva' and the *Lilium longiflorum* 'Osnat' (also known as 'Snow-Queen') that were bred by Ms. H. Yael and her coworkers. The *Gladiolus* cultivar 'Judith' bred by Dr. Vega was unique because it was not sensitive to geotropic bending of the flower stems. Another cultivar ('Hanna'), a triploid from a cross of a tetraploid commercial cultivar with the diploid wild *G. tristis*, was resistant to *Botrytis* and served as a prototype of the new group of "Orchidiolia" cultivars that were bred by Dr. A. Cohen and his coworkers. In the early 1980s, the diploid F₁-hybrids of *Anemone* were bred by Dr. Y. Ozeri and released for commercial production under the name "Jerusalem." In addition, a new group of triploid F₁-hybrid cultivars called 'Galil' were bred by Drs. N. Umiel, Y. Ozeri, and A. Hagiladi. Later, this research group released a group of *Ranunculus* cultivars ('Aviv' and 'Tomer') and a specially designed mix 'Aviv-Rainbow', for use not only in gardens but also as fresh-cut flowers. Recently, the Paperwhite *Narcissus* cultivars

‘Ariel’, ‘Inbal’, and ‘Nir’ were bred and released by Ms. H. Yael, Dr. A. Cohen, and Ms. D. Sandler-Ziv, and they are rapidly becoming popular in the international market. In cooperation with AGREXCO and some growers, D. Sandler-Ziv recently initiated a new breeding program for *Hippeastrum*.

The physiology of flowering and techniques for flowering control of *Narcissus*, *Gladiolus*, *Ranunculus*, *Zantedeschia*, *Ornithogalum*, *Paeonia*, and *Leucojum* have been studied. Protocols for the forcing and in vitro propagation of many ornamental geophytes have been developed (Lilien-Kipnis and Kochba 1987; Kamenetsky 2005, 2008; Cohen et al. 2008; Sandler-Ziv et al. 2008).

Experiments on propagation materials and fresh-cut flowers of ornamental geophytes in the Department of Postharvest Science of Fresh Produce have developed a database for optimal conditions and treatments during all postharvest phases, including prolonged storage and transport (Meir et al. 1995, 2004, 2005, 2007; Cohen et al. 1997; Droby et al. 1997; Philosoph-Hadas et al. 1997, 1999, 2000; Luria et al. 1998; Sandler-Ziv et al. 2000; Bernstein et al. 2005). These developments have maximized the postharvest life of the products and extended worldwide marketing season for cut flowers and propagation material.

Studies on the ecology and epidemiology of viral diseases affecting ornamental and cut flowers have conducted by Drs. G. Loebenstein, J. Cohen, and A. Gera (Gera and Cohen 1994; Cohen et al. 1996; Loebenstein 2006) in the Department of Plant Pathology of the Volcani Center.

4. Japan

Universities. In Japan, extensive research on flower bulbs has been conducted for many decades in several universities. Professor Emeritus H. Imanishi of Osaka Prefecture University and his associates focused on the control of flowering of many bulbous plants (Imanishi 2005). The forcing programs they developed are widely used by growers in Japan. One of the most important and practical studies was the research on the breaking of dormancy by ethylene (“smoking”) for Freesias and Dutch Irises. At present, Dr. H. Imanishi is continuing his research at the Tokyo University of Agriculture. Niigata University has a long history of research on plant breeding, physiology, biochemistry, and molecular biology, including gene transformation (JSHS 1998; Suzuki and Nakano 2002; Hoshi et al. 2004). Professor Emeritus K. Ohkawa of Shizuoka University also made significant contributions to the development of bulb industry in Japan (JSHS 1998). In addition, flower bulb research was started in early 1970s at Kyushu University, initially under supervision of Dr. S. Uemoto and then by Dr. H. Okubo, who is still actively

conducting research. This research has been quite basic and has led to over 50 scientific papers on flower bulbs. A major breakthrough in interspecific hybridization of *Lilium* species was the development of the technique of cut-style pollination combined with embryo culture by Y. Asano in Hokkaido University (Asano and Myodo 1977). At present, this technique is widely used for many other species.

Research Institutes. There are 47 prefectures in Japan, and each prefecture has agricultural research institute(s). The precise names vary by the prefectures, but most institutes have a part for ornamental horticulture. The focus of this research is primarily for the benefit of local farmers.

In Japan, commercial cut-flower production from flower bulbs started around 1910, and it increased rapidly after 1937. Low temperature treatments for Easter lilies and tulips were used for early or late flowering. The basic principles for control of flowering were established by H. Hosaka, T. Yamada, T. Matsukawa, S. Abe, and others (JSHS 1998) immediately after the World War II, mostly in the national and prefectural experimental stations (many have changed their names to “institute” or “research center”) in Japan.

Breeding of flower bulbs has been carried in some prefectures. The breeding of Easter lilies was carried out in the Kagoshima Prefecture, and new Asiatic hybrid cultivars were bred in the Niigata Prefecture. Tulip breeding was primarily concentrated in the Niigata and Toyama prefectures as well as at Niigata University. Among them, the most significant is Toyama Agricultural Research Center, where 30 tulip cultivars, including ‘Kikomachi’, were released. All of them are registered at the KAVB in the Netherlands.

5. South Africa. It is estimated that over 25% of the world’s ornamental flower bulb species originate in South Africa (Bailey 1976; Bryan 1989, 1995, 2002). In spite of this vast number of species, only gladioli and freesias are grown on a large scale in the commercial trade (Table 1.3). There are, however, several specialty bulbs that are commercially grown and widely available (e.g., *Agapanthus*, *Galtonia*, *Nerine*, several *Ornithogalum* species, including *O. dubium*, *Oxalis* spp., and *Zantedeschia*). Most of these species are not, however, grown extensively in South Africa. There are efforts to enlarge the number of commercial bulbs (www.hort.purdue.edu/newcrop/ncnu02/v5-076.html).

A primary research focus in South Africa has been the identification and botanical classification of the indigenous species (Du Plessis and Duncan 1989; Goldblatt and Manning 2000), which has been conducted

at the National Botanic Garden in Kirstenbosch. This has been an enormous undertaking due to the large number of species. In addition to contributing to this program, Duncan (1988) has written a comprehensive handbook on *Lachenalia*, which describes the species and some of its cultural requirements. The breeding and physiology of *Lachenalia* have been concentrated at the Vegetable and Ornamental Research Institute in Pretoria (Hancke and Coertze 1988; Niederweiser and van Staden 1990; Coertze et al. 1992; Roodbol and Niederwieser 1998; Du Toit et al. 2002, 2004; Kleynhans 2008). Subsequent to the review of *Nerines* by Van Brenk and Benschop (1993), Theron and Jacobs (1994a,b; 1996a,b) at the University of Stellenbosch published a series of studies on the physiology of *Nerine bowdenii*. This species is indigenous to South Africa and has commercial value as a landscape plant and fresh-cut flower.

The most widely grown bulbous crop in South Africa is the *Hippeastrum*, which originates in Central and South America (Traub 1958; Ellenbecker 1975). HADECO is a large bulb company in near Johannesburg, South Africa, that produces bulb crops for domestic markets and export. The company was established by Harry de Leeuw in 1948 (Barnhoorn 1995) and is currently owned by the Barnhoorn family (Barnhoorn 1976). HADECO initiated a *Hippeastrum* breeding program in 1948, and many cultivars with unique horticultural characteristics have been released. Therefore, their products are in demand worldwide.

6. United Kingdom. Flower bulbs, especially Narcissi, have a long history in the United Kingdom. As indicated in Section II.B, *N. pseudonarcissus* is native to England, and breeding was being conducted as early as the 16th century (Wylie 1952; Barr 1884). In addition, gardening and landscaping have long been popular in the the United Kingdom. Consequently, many gardening books in the the United Kingdom feature flower bulbs (Jefferson-Brown 1965, 1969; Doerflinger 1973; Genders 1973; Pavord 1999). Also, the Second International Symposium on Flower Bulbs (Rees and Van den Borg 1975) was held in the the United Kingdom in 1974 due to the large number of research and educational programs on flower bulbs that existed in the country at that time.

Bulb and fresh-cut flower production are centered in Cornwall, the Isles of Scilly, and Lincolnshire (Moore 1975; Tompsett 2006). Also, there has been some daffodil bulb production in Scotland (Turner 1975). The development of the commercial flower bulb industry has been greatly assisted by research conducted at the Glasshouse Crops Research Institute (GCRI) and Kirton and Rosewarne Experimental Horticultural Stations and technology transfer by the Agricultural Development

and Advisory Service (ADAS) of the Ministry of Agriculture, Fisheries and Food (MAFF). Unfortunately, most of these programs have been reduced or eliminated due to budget reductions that have led to closures of the stations and ADAS.

“The International Daffodil Checklist and Classified List” is maintained and published by the Royal Horticultural Society in London (Kington 1998). In addition, due to the existence of extensive breeding efforts by daffodil enthusiasts (Tompsett 2006), Barbara Fry initiated a daffodil breeding program at the Rosewarne Station in 1964 and continued until the station was closed in 1989 (Tompsett 2006). The focus was on early flowering and a large number of flowers per bulb (Fry 1975). Physiological and cultural research on *Narcissi* was conducted by A. Tompsett (2006) at the Rosewarne Station and by G. Hanks (1993) at the Kirton Station. They investigated many factors affecting the growth, development, and flowering of daffodils not only as forced bulbs but also for outdoor cut-flower production. The latter is very important in Cornwall and the Isles of Scilly.

Dr. A. Rees, who was at GCRI in Littlehampton, has published two books (Rees 1972, 1992) on flower bulb research. They have been invaluable contributions to the global flower bulb industry and cover most of the physiological and pathological research conducted at GCRI.

Cheal and his colleagues (1962, 1963, 1964, 1996a,b, 1968, 1969) conducted a series of studies on the nutrition of tulips at the Long Ashton Experiment Station. This research, and that of Amaki and Hagiya in Japan 1960a,b, established the periods of nutrient uptake and the effects of nitrogen (N), phosphorus (P), and potassium (K) and some of the minor elements on the growth, development, and flowering of the tulip.

Without question, the research conducted at ADAS and MAFF has been a valuable resource for the flower bulb industry not only in the United Kingdom but also globally. The scientists have produced or assisted in producing many publications on flower bulb production (Wallis and Mather 1977; Moore 1984; Gilbert 1985), cut flower production and forcing (Brown 1967; Briggs 1972, 1976a,b; Grower Guide 1981; Flint 1985; ADAS 1983, 1985b), and pest control (Morgan et al. 1979; Moore et al. 1979; Lane 1984; Penna et al. 1984). They also produced a manual for forcing bulbs as potted plants (Anon. 1985).

7. United States

The Land-Grant Universities. The first land-grant university established in the United States was the Michigan Agricultural College, now Michigan State University at East Lansing. It was established in 1855 by the State of Michigan in order to provide an institution of higher learning to

assist the state's agricultural community (Dennis et al. 2007). Subsequently, the U.S. Congress passed the Morrill Act (also known as the Land-Grant College Act), which was signed by President Abraham Lincoln on July 2, 1862. This act established agriculturally oriented universities in all states and provided the mechanism and support for research, teaching, and technology transfer programs. Since its inception, this has been an incredibly effective system, and the flower bulb industry has benefited from the research conducted at many land-grant universities. Some of the most significant flower bulb research programs are summarized below.

Without question, the most researched flower bulb in the United States has been *Lilium longiflorum* (Kiplinger and Langhans 1967; Miller 1992, 1993). Over the years, major programs were concentrated at Cornell University, Michigan State University, Oregon State University, the Ohio State University, and several campuses of the University of California. The primary goal was to produce bulbs that could be field-grown and subsequently forced in greenhouses for Easter as flowering potted plants. Research on hybrid lilies has been more limited (Beattie and White 1993; Miller 1992), and most of the programs have been on plant breeding (McRae 1998).

Research on spring-flowering bulbs has been located primarily at Cornell University, Michigan State University, North Carolina State University, and Washington State University (Gould 1957, 1993; De Hertogh and Le Nard 1993b; De Hertogh 1996). This research has focused not only on aspects of bulb production but also on forcing and landscaping. In addition, almost all spring-flowering bulbs, most of which are Dutch-grown, have been included in these programs.

Gladiolus research has been conducted primarily at the University of Florida (Koenig and Crowley 1972; Cohat 1993). The primary goals were to control all major diseases and insects (Magie and Poe 1972) and to produce high-quality fresh-cut flowers (Marousky and Woltz 1971) for North American markets.

Postharvest research on flower bulbs and selected perennials has been focused not only on fresh-cut flowers but also flowering potted plants. This research has been concentrated at the University of California at Davis, the University of Florida, Michigan State University, North Carolina State University, and Rutgers University. The information has been published not only in scientific journals but also in several books (Nell 1993; Sacalis 1993; De Hertogh 1996; Nell and Reid 2000; Hamrick 2003).

U.S. Governmental Agencies (USDA/APHIS/ARS). The United States Department of Agriculture (USDA) has two agencies with components

that are important to the flower bulb industry. The Animal and Plant Health Inspection Service (USDA/APHIS) inspects flower bulbs prior to shipping. This agency is also responsible for inspecting all agricultural imports to the United States. The USDA is also charged with conducting research within the USDA/Agricultural Research Service (USDA/ARS), which has research facilities in Beltsville, Maryland, and at selected land-grant universities (see Section V.7 a) that are located in all 50 states. The USDA/APHIS is responsible for inspecting flower bulbs as directed by Plant Quarantine 37. In 1926, it was responsible for enforcing the embargo on *Narcissus* bulbs due to nematodes. This embargo led to a significant increase in domestic flower bulb production, which has continued into the 21st century. In the late 1940s, the Netherlands Flower Bulb Institute, directed by Gustave Springer, entered into an agreement with the USDA/APHIS to pre-inspect the flower bulbs. This agreement has allowed bulbs from the Netherlands to be inspected prior to being transported to the United States. This system has been expanded to include other countries and is still being utilized. All costs for this service are covered by the flower bulb industry in the production country.

Flower bulb production research has been integrated in the USDA/ARS for over a century (Gould 1957, 1993). The first commercial planting of spring-flowering bulbs in the State of Washington was by George W. Gibbs in 1892. In 1905, the USDA provided bulbs for the first research trials (Gould 1993). Subsequently, starting in 1916, Dr. D. Griffiths, who was stationed in Beltsville, Maryland, initiated his research at the USDA Research Station in Bellingham, Washington. He continued the research until 1936 and wrote several publications on flower bulb growing and forcing (Griffiths 1922, 1924, 1926, 1928, 1936a,b). After World War II, in cooperation with the Northwest Bulb Growers Association (NWBGA), research was conducted by Dr. N. Stuart and Dr. R. Doss of the USDA and Dr. C. Gould, Dr. R. Byther, and Dr. G. Chastagner of the Western Washington Research and Extension Center (WWREC) in Puyallup, Washington. This research focused on all factors affecting bulb growing and forcing (Gould 1957, 1993) and the control of diseases (Gould and Byther 1979a,b,c). Currently, with the reduced levels of funding, the primary focus is only on pest management (Byther and Chastagner 1993) in Puyallup and biotechnology at the USDA in Beltsville, Maryland. Most U.S. flower bulb production (e.g., lilies, tulips, *Narcissus*, *Ranunculus*) is concentrated in the coastal areas from San Diego to the Canadian border. In addition, gladioli are produced in Florida, New Jersey, and Michigan, and caladiums are produced in Florida.

8. Other Countries. In addition to the research programs described in just described, there are or have been significant flower bulb research programs elsewhere in the world. Many have been reviewed either by De Hertogh and Le Nard (1993b) and their colleagues or published in the 10 symposia of the International Society for Horticultural Science (ISHS) that have focused on flower bulb research and educational programs (Bergman et al. 1971; Rees and van der Borg 1975; Rasmussen 1980; Bogers and Bergman 1986; Doss et al. 1990; Saniewski et al. 1992; Lilien-Kipnis et al. 1997; Littejohn et al. 2002; Okubo et al. 2005; Van den Ende and Gude 2009, in press). Within this group, there are several significant programs that have impacted the global industry.

In Poland, Dr. M. Saniewski and his coworkers have contributed greatly to our understanding of the physiology and, especially plant growth regulators, of tulips (Saniewski and De Munk 1981; Saniewski and Kawa-Miszczak 1992) and hyacinths (Nowak and Rudnicki 1993). In addition, Mynett (1992) and colleagues have conducted plant breeding studies on a wide range of flower bulbs.

In New Zealand, several excellent programs have been developed on flower bulbs. There have been major efforts on the breeding and physiology of *Zantedeschia* (Funnell 1993), a South African species. These studies have resulted in a marked reemergence of this species in the cut-flower and potted plant markets. Consequently, there are commercial centers of production and breeding in the United States and the Netherlands. New Zealand researchers have also carried out intensive studies on *Sandersonia* (Catley et al. 2002; Morgan et al. 2002), another South African species. It has not, however, been as widely commercialized as the Calla lily.

There are emerging internationally based programs that will, it is hoped, be successful. They are located in Brazil (Meerow et al. 2002), Chile (Bridgen et al. 2002), and Turkey (Baktir, 2008). These countries have many indigenous flower bulbs (Tombolato et al. 1992; Bryan 1994; Bridgen et al. 2002; Baktir, 2008) and have enormous potential for commercial flower bulb and bulb flower production. This research must be conducted to support their flower bulb industries and bring new products to the world marketplace.

C. Flower Bulb Exhibitions

1. General Aspects. Public flower exhibitions are an excellent forum to stimulate consumers to purchase and utilize flower bulbs not only for gardens and landscapes but also as forced products (e.g., fresh-cut flowers and potted plants). The first exhibition in the Netherlands was

organized in Haarlem in 1818, and the first exhibition outside the Netherlands was in Belgium in 1839 (Krelage 1946). Thus, there is a long history of usage of flower bulbs in these settings. Here we cover some of the well-known exhibitions.

2. Special Flower Bulb Gardens. Without question, the most extensive and well-known flower bulb garden in the world is the Keukenhof (www.keukenhof.nl) located in Lisse, the Netherlands (the heart of the Bulb District). The garden was established in 1949 by 11 bulb growers, who wanted to show their cultivars primarily to other growers and exporters. Wisely, they also included the public. In the spring of 1950, the first flowering season, over 200,000 visitors went to see the displays. Thus, the primary orientation was immediately changed from the industry to the general public. In 1950, a greenhouse was constructed for indoor exhibitions, and a windmill was brought from the province of Groningen in 1956. Today, the garden contains over 32 hectares and, annually, attracts about 800,000 people from the world over.

In addition to the Keukenhof, Hortus Bulborum (www.hortus-bulborum.nl), located in Limmen, North Holland, the Netherlands, is very special bulb garden that is open to the public (see Section IV.B.3). Started in 1928 (Leijenhorst 2004), it contains collections of old cultivars of tulips, hyacinths, daffodils, and specialty bulbs, such as crocuses. The bulbs are not only unique but also can be used as germplasm for the breeding of new cultivars.

3. Other Public Gardens. In England, at least two major gardens feature flower bulbs as part of their programs: Springfield's Festival Gardens (www.gardenvisit.com/g/spr) in Spalding, Lincolnshire, which was remodeled in 2003–2004, and the Easton Walled Gardens (www.eastonwalledgardens.co.uk) in Grantham, Lincolnshire. In addition, Hampton Court, which is located outside London, normally has large flower bulb displays in the court gardens. In Canada, Butchart Gardens (www.britishcolumbia.com/attractions) has a large display of spring- and summer- flowering bulbs. The garden is truly worth a visit and is located outside Victoria, Vancouver Island, British Columbia. Also, in Ottawa, there is an annual display of tulips that are provided by the Dutch royal family in appreciation for Canada's assistance during World War II. In the United States, Longwood Gardens (www.longwoodgardens.org) in Kennett Square, Pennsylvania, features bulbs not only in the gardens but also in its large conservatories and greenhouses. In Japan, the Tonami Tulip Fair in Tonami City, Toyama Prefecture, exhibits about 450 cultivars in late April to early May every year. The unique World Lily Gardens of Yurigahara Park is located in Sapporo, Hokkaido. It is open 24 hours

year-round and is free of charge. About 100 lily species and cultivars are grown outdoors, and the flowering season lasts for 4 months from early June to late September. Because of the large indigenous population of flower bulbs in South Africa, the National Botanic Gardens at Kirstenbosch always has bulbs in flower, either in the gardens or in the greenhouses (Du Plessis and Duncan 1989; Goldblatt and Manning 2000).

4. Other Flower Exhibitions and Parades. There are about 300 annual indoor/outdoor flower bulb exhibitions in the Netherlands (www.dutchflowerlink.nl). Some of the primary ones include:

- Midwinterflora (www.midwinterflora.nl) in Lisse in January
- Creilerflora (www.creilerflora.nl) in Creil in February
- Westerkoggeflora in de Goorn in January
- Driebanflora in Venhuizen in January
- Lenteweelde in Obdam in February
- Holland Flowers Festival (www.hollandflowerfestival.nl) in Bovenkarspel in February
- Lentetuin Breezand (www.lentetuin.nl) in early March in Breezand.

In England, the Chelsea Flower Show is held annually in May and is sponsored by the Royal Horticultural Society (www.rhs.org.uk). Forced bulbs are an integral part of all these exhibitions. In the State of Washington, the Puyallup Valley Daffodil Festival and the Skagit Valley Tulip Festival are held in April and attract about 500,000 visitors annually.

In the Netherlands, an annual Flower Parade (www.bloemencorso-bloembollenstreek.nl) was first organized in 1948 and is held in late April. The parade starts in Noordwijk and ends in Haarlem, attracting over 1 million viewers along the route. Also, each year there are local competitions of floral mosaics in villages in North Holland. The mosaics have a special theme and are constructed primarily with hyacinths florets. Every 10 years, the Dutch ornamentals industry organizes a Floriade—a six month ornamental show (indoor and outdoor)—in a selected city in the Netherlands. The floriades started in 1962; the next one is scheduled for 2012 in Venlo in the province of Limburg. Each fall, the Horti-Fair is held in Amsterdam, attracting about 50,000 visitors. Flower bulbs are also featured in this exhibition.

D. Ornamental Geophyte Societies

Over the centuries, many flower bulb societies have been founded in North American and Europe. They contribute to the global dimension

Table 1.10. List of selected societies for ornamental geophytes (flower bulbs).

Geophyte	Society	Website
All ornamental geophytes	International Bulb Society	www.bulbsociety.org
Dahlia	Royal Horticultural Society	http://www.rhs.org.uk/index.asp
	American Dahlia Society	www.dahlia.org
	Nederlandse Dahlia Vereniging	www.nederlandsedahliavereniging.nl
Gladiolus	North American Gladiolus Council	www.gladworld.org
Iris	American Iris Society	www.iris.org
	British Iris Society	www.britishtirissociety.org.uk
Lilium	North American Lily Society	www.lilies.org
Narcissus	American Daffodil Society	www.daffodilusa.org
	The Daffodil Society of The United Kingdom	www.daffsoc.freemove.co.uk
Peony	American Peony Society	www.americanpeonysociety.org
Ranunculaceae	The Ranunculaceae Society, Dublin, Ireland	http://homepage.eircom.net/ranunculaceae
Tulip	Wakefield and North of England Tulip Society	http://www.tulipsociety.co.uk/

of the ornamental industry (Table 1.10; Doerflinger 1973). These societies publish a variety of newsletters, yearbooks, bulletins, and books (Fairchild 1979; Howie 1984; Koenig and Crowley 1972) related to plant collections, the identification and taxonomy of indigenous species, and the breeding and release of new cultivars. In addition, most have annual meetings to exchange information and plant materials, show new cultivars, and present special awards. One worldwide society that is dedicated to the dissemination of knowledge and conservations of flower bulbs is the International Bulb Society (www.bulbsociety.org), which publishes the journal *Herbertia* and annually awards the Herbert Medal for the significant contributions to the knowledge and importance of flower bulbs.

VI. CONCLUSIONS AND FUTURE RESEARCH

During the past decades, the competition for existing flower bulb markets has been constantly increasing. Consequently, demand has increased for high-quality bulbs and bulb flowers. In addition, the globalization of the horticultural trade has led to advances in the transfer of knowledge and economic progress in developing countries. Thus, bulb production is no longer limited to countries with temperate climates. The produc-

tion of bulbs and bulb flowers of high quality in regions with warm climates has become significant during the last decade. This production has been promoted by relatively inexpensive land, low labor costs, and the expansion of international trade. These developments have presented not only a challenge to the bulb industry; they also have produced changes in research programs. Multidisciplinary approaches are required for the improvement of existing crops and for potentially useful species and their development into new commercial crops and novel products. This paradigm has led to the initiation of studies dealing with physiological and biochemical aspects of internal and environmental regulation of geophyte development.

A. Search, Evaluation, and the Utilization of New Crops

There have been numerous efforts to search for and introduce new ornamental geophytes (see Section III.D). Some have already gained popularity, but some have not yet appeared in the markets. There are still regions in the world where expeditions for indigenous species need to be expanded and, especially, continued.

Taxonomic studies and classifications of geophytes, of either known or newly introduced species, are important. Currently, studies using classical or molecular approaches are limited (Meerow 2002; Duncan et al. 2005; Hayashi and Kawano 2005). Clarifying the geographic distribution of wild geophyte species and their genetic diversity is important not only for breeding studies but also for the conservation of rare and endangered species.

Reevaluation of known geophytes is also necessary in their natural habitats both for conservation purposes and for obtaining information, such as the finding of self-compatible *Lilium longiflorum* (see Section IV. B.5).

B. Environmental Issues and Integrated Pest Management

Global climatic changes are expected to continue and will affect bulb production and utilization. One of the major effects will be an increase in the incidence of disease. Also, a shift of production areas may occur. Flower bulb researchers cannot provide the solution to climate changes. They can, however, contribute by developing culture systems, integrated pest management, and sustainability practices and breeding programs to reduce the energy involved in bulb and bulb flower production.

Physiological studies on desiccation and drought consequences and on high- and low-temperature stresses will become more important

and must be intensively explored. Research on growth control without usage of the PGR and disease control by replacing the need for soil fumigation without the use of pesticides is also necessary. These programs will lead to environmentally friendly and sustainable production systems. They also may be useful for improving performance of bulbs in gardens and landscapes.

C. Production of Propagation Materials

Physiologically mature and disease- and insect-free propagation material is necessary to obtain high-quality marketable bulbs and flowers. The bulb size (quantity of reserves) is a reflection of photosynthesis and is one of the first criteria for quality. Research on photosynthesis in relation to various production conditions is needed. Light and temperature are the most limiting factors for photosynthesis. Thus, for bulb production in warmer climate areas, which is expected to increase in the future, higher night temperatures will be challenging. This will be due to higher level of leaf respiration at night and can result in reduced bulb yields and quality.

Several nondestructive monitoring systems using light- or sound-reflecting sensors have been developed to determine the best time to market some of the tree and vegetable fruits (orange, watermelon, etc.) (Abbott et al. 1997). Various parameters have been proposed for successful cold treatment of tulip bulbs. They include starch and alpha-amylase (Gorin and Heidema 1985), chalcones (Gorin et al. 1990; Franssen and Kersten 1992), polyamines (Kollöffel et al. 1992), mitochondria (Hobson 1979; Kannevorff and Van der Plas 1990), amino acids (Le Nard and Fiala 1990; Tonecki and Gorin 1990), 4-methylene-glutamine:asparagine ratio (Lambrechts et al. 1992) and nuclear magnetic resonance (NMR) images (Okubo et al. 1997; Van der Toorn et al. 2000; Kamenetsky et al. 2003b). The development of mechanical, biophysical, or biochemical sensors or markers for monitoring of invisible but critical parameters, such as bulb health and maturity, the status of intrabulb flower development and dormancy, and the termination of the cold-week requirements, is urgently needed. The search for marker genes as sensors is another technique needed to measure bulb quality. To be practical, these techniques must be inexpensive and reliable.

D. "Dormancy"

One of the most important phases in the life cycle of a geophyte is the formation and development of the storage organ and its related

“dormancy” period. The definition of dormancy varies and is not universally understood and accepted. Dormancy in geophytes generally is recognized using broad definitions, such as the state of bulbs where growth is not visible. In contrast, there are also opposing views. For example, there is no dormant state in *Lilium longiflorum* bulbs (Miller 1993), because a meristem is continually initiating new scale, leaf, or flower primordia throughout the year (Blaney and Roberts 1966). Thus, the terms *dormancy* and *dormancy release* (breaking) are broadly and loosely used from the beginning of bulb formation to the fulfillment of the temperature requirements after flower bud initiation and development. One of the latest suggestions for establishing dormancy concept proposes that the induction of dormancy and the induction of bulb formation are the same phenomenon (Okubo 2000). In the future, it will be important to develop common concepts and terminology for all flower bulb researchers to use.

Physiological aspects of low- and high-temperature requirements have been studied intensively in the major geophytes but have focused primarily on commercial bulb production. However, the mechanism of dormancy release by low or high temperatures is still unclear, and additional research is clearly needed. It has been shown that alpha-amylase activity and sucrose content increased during the cold storage period in hyacinth shoots (Sato et al. 2006). A cDNA for a cold-responsive alpha-amylase gene was isolated, and its expression increased in scales during cold storage. The promoter region of the gene that contained the CArG (a cold-responsive) element, which is related to the response to low temperatures, was also found. This finding is quite different from the well-known responses in tulips and has enhanced progress in controlling dormancy. Transformation using such genes may make dormancy-breaking control practical and useful to the industry.

E. Florogenesis and Stalk Elongation

Elucidating the genetic control of florogenesis in flowering bulbs is important not only for the understanding of their developmental biology but also for their agronomic and economic importance. Florogenesis of bulbous species is affected by the genetics of the individual plant and by environmental factors. These interactions affect a series of molecular and biochemical processes leading to the transition of the plant from a vegetative state to a reproductive state. The morphological and physiological aspects of florogenesis have been studied in several economically important bulbous species (Rees 1992; De Hertogh and Le Nard 1993b). However, there is limited information on the genetic

control of meristem transition and subsequent formation of the inflorescence or individual flowers and the flower parts. Recent reports demonstrate that flower development of ornamental bulbs is controlled differently from the model plants such as *Arabidopsis* or *Antirrhinum* (Flaishman and Kamenetsky 2006; Noy-Porat et al. 2007; Rotem et al. 2007;). However, the homologues of *LFY*, one of key genes in floral initiation and differentiation in *Arabidopsis*, were recently found in *Narcissus*, hyacinths, and *Lilium candidum* (Noy-Porat et al. 2007; Zaccai et al. 2008). Understanding the mechanisms controlling the transition of apical meristem from the vegetative to reproductive state will facilitate the shortening of the juvenile period (see Section IV.B).

Most ornamental geophytes form inflorescences. Hence, modification of the genes controlling inflorescence development might affect the inflorescence and flower architecture. Thus, more information on the genetic control of inflorescence development is needed. Recently, several genes involved into differentiation of the individual flower in *Lilium longiflorum* were shown to be homologous to the genes of the ABCDE model that was developed for *Arabidopsis* and other model species (Benedito et al. 2004a). Molecular characterization of genes involved in flower morphology could help to develop novel floral architectures in bulbous plants by classical breeding techniques or by genetic manipulation using transformation systems.

In order to obtain desired marketable length of the flower stalks (scapes) in ornamental geophytes (i.e., longer for cut flowers and shorter for potted plants), increased knowledge of the mechanisms controlling scape elongation is necessary. Some hypotheses on hormonal control of the elongation growth have been proposed, but the mechanism has not been elucidated. Thus far, the accumulation of knowledge on flower bulbs has been primarily concentrated on a few genera (*Hyacinthus*, *Gladiolus*, *Lilium*, *Narcissus*, *Tulipa*) and/or limited to specific topics (Le Nard and De Hertogh 1993a). Emphasis, however, must be given to specialty bulb crops. They can yield new information that can be used for basic studies. Currently, the information related to specialty crops is very limited. For example, it is known that the low temperatures are required for the elongation of leaves and stem in tulips and hyacinths, whereas in *Muscari*, only flower stalk elongation requires low temperatures; leaves can grow without low temperatures (Rudnicki and Nowak 1993). Such organ-dependent differential responses to temperature that differ from the tulip should be compared using other species. It is clear that growth is controlled by plant hormones; this has been confirmed by studies using exogenous plant growth regulators. However,

additional research, particularly on endogenous levels, is necessary. Genes controlling plant hormones have been recently clarified by Wu et al. (1996), and a molecular approach may open new research directions. Studies on metabolism of carbohydrates and their degradation and synthesis by studying gene expression levels are also future research topics.

F. Breeding

Besides the breeding programs related the control of flowering and dormancy that have been described, the most important and required goal for breeders is disease, and especially virus, resistance. The use of pesticides has and will continue to become more restricted in many countries.

A difficulty in the breeding of many geophytes is their long juvenile period (see Section IV.B). Thus, the use of molecular approaches, such as marker genes linked to targeted characters, becomes very important and can shorten the breeding cycle. Recent studies suggest that the some genes (e.g., the *Arabidopsis* FLOWERING LOCUS T (*FT*) gene and its homologues) are involved in reduction of juvenile stage and promoting flowering in younger plants in some species (Kotoda et al. 2002; Endo et al. 2005). However, currently, it is not certain whether it is applicable to geophytes and other perennial herbaceous plants. Since most flower bulbs must reach a critical bulb size (a minimum amount of storage reserves) prior to floral induction, transformation of only early-flower-inducing gene(s) may not be sufficient. Also, even if earlier flowering is achieved, flower quality may be poor and, thus, not marketable. However, the technique should be useful for new qualitative characters, such as color or flower shape. Finding of the marker genes linked to these characters will assist in making selections.

Since virus transmission is possible not only through conventional propagation methods, such as scaling, but also through in vitro propagation, future breeding programs should concentrate on virus resistant cultivars. Another solution would be an establishment of seed propagation systems. Such a strategy has been accomplished using *Lilium formosanum*, which can flower from seed in one vegetative season (Saruwatari et al. 2008). An interspecific hybrid of *L. formosanum* $\times$ *L. longiflorum* (= *L. $\times$ formolongi*) has been incorporated into the year-round cultivation system of the Easter lily in Japan, and it is on the market in summer season (Imanishi 2005). This lily hybrid is propagated by seed. Similar approaches should be evaluated for other geophytes.

G. Model Plant for Molecular and Genetic Research

The need to increase research on molecular and genetic mechanisms of geophyte development is clear. Since no bulbous *Arabidopsis* species is available, an alternative model plant is needed for future dormancy and florogenesis research in bulbs. Scientists involved in these studies should discuss and select a model geophyte species.

At this stage, most of genetic studies on florogenesis have been performed on commercially important crops, such as lilies, Narcissi, or tulips. However, in addition to being economically important, a model species has to have several criteria: a short juvenile period, easy pollination and seed germination, well-known morphological and physiological aspects (especially on florogenesis and dormancy), an established transformation system, and rapid regeneration ability (Flaishman and Kamenetsky 2006).

For the dormancy studies, the major problem regarding the control of bulbing is that once a plant begins initiating bulbs, it is difficult to reverse the process. Thus, the model plant should be controlled either environmentally or genetically. It is possible that Dutch iris can serve as a model (Okubo and Uemoto 1981). Recently, lotus plant *Nelumbo nucifera*, an aquatic ornamental and edible rhizomatous plant, was found to be suitable (Masuda et al. 2003, 2007). The rhizome stops elongating and starts enlarging under short days, but if exposed to long days, the apical meristem on the top end of the swollen internode of the rhizome resumes elongation.

Ornithogalum dubium, a relatively new ornamental crop from South Africa and currently cultivated mainly in Israel and the United States, also meets the necessary criteria. It too can be used as a model plant for biochemical and genetic aspects of florogenesis in bulbous ornamental crops.

An alternative candidate would be a genetically controllable species, which should have bulb-forming and non-bulb-forming phenotypes within different cultivars. It must be able to be bred and produce progenies that are fertile. For example, recently obtained populations of garlic seedlings (Kamenetsky et al. 2003a) demonstrate a large variation in vegetative and reproductive characters—including bulbing ability, bulb color and size, the number of cloves, and response to environmental conditions—that are similar to the gene pool of vegetatively propagated garlic clones. The availability of the large variability, recently produced by sexual reproduction, opens new approaches for genetic studies (Shemesh et al. 2008). After establishing model plants and control systems, molecular approaches to understand dormancy and florogenesis should be possible.

H. Flower Quality, Postharvest Handling, and Transportation

Longevity is a major factor of flower quality. Numerous studies have been carried out to find the mechanisms of flower senescence and methods to lengthen vase life by chemical applications. It has been a concern that increasing flower longevity of fresh-cut flowers can potentially create a marketing problem, because the longer vase life may affect the frequency that consumers buy cut flowers. In fact, the opposite is probably true. Thus, flower life is one of the important research objectives for breeders. The use of chemicals for that purpose becomes prohibitive in order to avoid environmental effects. More research for alternative and environmentally friendly but inexpensive substitutes is needed.

I. Propagation

Effective propagation systems, including in vitro propagation, need to be developed for many bulb crops. In vitro propagation remains expensive, depends on countries with low labor costs, and still has not become a final solution to all problems. The cost of in vitro propagation increases with the economy development in developing countries. Without more efficient propagation systems, industry must keep searching for the low-labor-cost countries.

J. Research Network

The research areas described in this chapter are all closely related. Thus, future research must be interdisciplinary and international. Knowledge exchange between science and industry and establishment of public-private partnership are important. The Symposia of the International Society of Horticultural Science (ISHS) are held in various regions in the world every four years. The ISHS's International Symposia on Flower Bulbs (from 2008; International Symposium on Flower Bulbs and Herbaceous Perennials) are an excellent opportunity for flower bulb researchers to communicate and to exchange information. However, not all scientists can attend the symposia due to economic and time constraints. Thus, the Internet must be used effectively. The establishment of a global network system by bulb researchers, growers, and marketers is one of the priorities of the ISHS Working Group on Flower Bulbs and Herbaceous Perennials. (The chairman is Dr. William B. Miller, Cornell University.) Publishing Web newsletters or opening the board for exchanging information and opinions (chat room) will be the first step of this network.

In conclusion, it is apparent that past research has significantly impacted the development of a global flower bulb industry. It is vital,

however, that the research must continue not only for the benefits of the floricultural industry but also for a healthy environment and the well-being of the public.

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