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Herbaceous Peony (*Paeonia*): Genetics, Physiology and Cut Flower Production

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ABSTRACT

Peony (*Paeonia* spp.) is one of the most popular garden plants in temperate regions. They were introduced into cultivation in China hundreds of years ago, and have since been spread widely to many countries. According to morphological traits and life form, the genus is divided into tree and herbaceous peonies. Numerous cultivars of herbaceous peonies have been developed to satisfy demand for colors, fragrance, flowering time, and disease resistance. In the last two decades, the popularity of peonies as cut flowers has resurged, and has resulted in additional requirement for new research, production methods and postharvest technology. Today, more than 25 countries produce cut peony flowers, with the primary markets being in Europe and the USA. Despite the popularity of herbaceous peonies, their production and use are restricted due to a lack of reliable systems for mass propagation, a long juvenile period, complicated flowering physiology and ineffective postharvest handling procedures. In this review, highlights of the recent scientific research in herbaceous peony are presented, along with up-to-date information on peony propagation, postharvest handling and cut flower marketing.

Keywords: chilling requirements, geophyte, florogenesis, *Paeonia*, postharvest

Abbreviations: **ABA**, abscisic acid; **BA**, 6-benzyladenine; **GA**, gibberellic acid; **IAA**, indole-3-acetic acid; **IBA**, indole-3-butyric acid; **KT**, kinetin; **NAA**, α-naphthaleneacetic acid; **TDZ**, thidiazuron; **STS**, silver thiosulfate

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INTRODUCTION

The peony (*Paeonia* spp.) has a long-standing reputation as the "queen of the garden" in many countries and continents. In China, peonies were in cultivation 3,000 years ago. The Chinese chose it as the principal flower in the Imperial Palace Gardens, calling it “Sho Yo,” meaning “Most Beautiful” (Gast 1995). Missionary Buddhist monks brought knowledge of the peony to Japan, where, to this day, it is a symbol of prosperity and wealth. In Greek mythology, the

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Invited Review

Table 1 Common names, geographical distribution and natural habitats of selected herbaceous peonies. Data adapted from Andrieu and Debussche 2007; efloras.org. 2011; Halda and Waddick 2004

***Paeonia* species** **Common name**	**Geographical distribution**	**Habitat**
P. anomala L.	European part of Russia, Siberia, Central Asia northwestern China and Mongolia	Forests, meadows, slopes in the mountains
P. californica Torrey & A. Gray **California Peony**	Endemic to southwest California	Dry hillsides and chaparral communities of the coastal mountains
P. caucasica (Schipcz.) Schipcz.	Caucasus, western and central regions	Mountain forests, meadows, up to subalpine zones
P. daurica Andr.	Crimea, northwestern Caucasus	Mountain forests, grassy slopes
P. japonica (Makino.) Miyabe.&Takeda **Japanese Peony**	Northern Japan	Mountains, forests of deciduous trees
P. lactiflora Pall. **Chinese Peony**	Siberia (Dahuria), Far East, Mongolia, China, Korea	Open forest edges, stony slopes of subalpine zone
P. macrophylla (Albov) Lomak.	Caucasus, central and western regions	Mountain forests, clearings, meadows
P. mascula (L.) Mill. **Balkan Peony**	Italy, Morocco, Spain, Greece, Turkey	Bushy places in meadows and hills
P. mlokosewitschii Lomak. **Golden Peony**	Caucasus, Dagestan	Mountain forests, stony slopes in middle and upper mountain zones
P. officinalis L. **European Peony**	Europe to Central Asia	Open and semi-open slopes, forest and shrub land
P. tenuifolia L. **Fern-leaf Peony**	Southern and central regions of Europe, Caucasus, the Balkan Peninsula	In steppes, among shrubs on slopes
P. wittmanniana Hartwiss ex Lindl	Caucasus (Abkhazia)	Mountain forests, clearings

plant was named after Paeon, a student of Asclepius, the Greek god of medicine and healing (Rogers 2000).

According to morphological traits and life form, the genus is divided into tree and herbaceous peonies. By the early 19th century, herbaceous peony had been widely introduced into European gardens from China and Japan, and by the 1850s many American nurseries began offering new cultivars of herbaceous peonies to their customers. Today, gardeners throughout Europe, Asia and North America regard the peony as one of the most beautiful and rewarding plants to grow. Not only are herbaceous peonies grown as garden ornamentals, but they also have a long history of use as traditional medicinal plants (Rogers 2000). Recently, a surge in interest in natural bioactive compounds for medical uses has led to research on essential oils and antioxidant potentials of the root extracts (Orhan *et al*. 2010), and determined peonies as a possible source of oleanolic and ursolic acid (Zhou *et al*. 2011). In oriental medicine, peony is used clinically to treat depression-like symptoms, and has been shown to possess anti-depressant property in various test models using laboratory animals. Modern research delineates the active chemical compounds of peonies, determines the pharmacokinetics, establishes the toxicological profile, and assesses the potentials of peony in clinical applications (Mao *et al*. 2012). The medicinal traits and possible uses of peony will not be discussed in this review.

Despite the popularity of peonies as cut flowers and potted plants, several reasons restrict its production and use, such as the lack of reliable systems for rapid propagation, a long juvenile period, a complex flowering physiology, and the control of botrytis during postharvest handling. Cut peony flowers are highly valued in world markets, but availability is limited to only a short period in late spring and early summer at any one production location.

Peonies are grown successfully in temperate, cold-winter climatic zones (generally USDA cold hardiness zones 3-8, but some types will survive in zone 1). In the 1980s, Byrne and Halevy (1986) reported on the possibility of producing herbaceous peonies under warmer conditions and this research initiated development of peony cultivation in Israel, Italy and southeastern France. Concurrently, peony cultivation for cut flower production began in the Southern Hemisphere (New Zealand, Chile and Argentina), and recently, a new peony project was initiated in Alaska to bridge cut stem production between that in Northern Europe and mainland USA with that in the Southern Hemisphere. However, we have learned that for successful commercial production, comprehensive studies of plant development and flowering physiology of peony are essential. In this review, highlights of the recent research on herbaceous peony are presented, along with current information on peony propagation, postharvest and cut flower marketing.

TAXONOMY AND GEOGRAPHICAL DISTRIBUTION

The genus *Paeonia* belongs to the family Paeoniaceae and consists of more than 30 woody and herbaceous species, native to Asia, southern Europe and western North America (Halda *et al*. 2004). Tree peonies are popular as garden plants in China, Japan, the USA, Canada, and Europe. These plants have woody stems, grow to approximately 2 m, and flower in early spring. Herbaceous peonies are shorter, with annual stems arising from underground storage organs, and flower in late spring and early summer.

The taxonomy of the genus *Paeonia* has been a subject of numerous discussions and revisions, although this has recently been greatly clarified by Ji *et al*. (2012). For many years, the genus was considered to be a part of the family Ranunculaceae, but now it is generally accepted that the genus *Paeonia* belongs to the family Paeoniaceae. Within the genus, classification of the species has also changed several times with increasing access to plant material and publications of Russian and Chinese botanists by Western taxonomists and vice versa. Today, however, plant material is more readily available for study from regions where large populations of wild peonies exist.

The most widely used classification system for the genus *Paeonia* in western countries is the system developed by the English peony expert, Sir Frederick J. Stern (1946). He divided the genus into 3 sections, 4 subsections, 16 groups, 33 species and 13 botanical varieties**.** Halda *et al*. (2004) documented 25 species, including 40 subspecies and varieties. Some sources, mostly from the Internet, describe between 35 and 50 different species of the genus *Paeonia*. Geographical distribution and natural habitats of the most well known herbaceous species are presented in **Table 1**.

A number of species (*P. officinalis*, *P. mascula*) are tetraploid and exhibit considerable variation (Page 1997). Classification of species and popular cultivars was also proposed based on the morphological characters, patterns of flavone/flavonol compounds in the petals (Hosoki *et al.* 1991) or DNA analysis (Hosoki *et al.* 1997). Random amplified polymorphic DNA (RAPD) analysis was performed to classify 21 herbaceous peony cultivars or species (Hosoki

Fig. 1 Morphological structure of herbaceous peony. (**A**) Entire plant prior to flowering. Numerous monocarpic shoots are developing from the underground crown. April 2009, Israel. (**B**) Schematic presentation of the monocarpic shoot (adapted from Cheng *et al.* 2009b). (**C**) Renewal buds ("eyes"), developing on underground crown. Usually the renewal buds are formed at the basis of the annual stems. November 2008, Israel. (**D**) Underground organs: crown, storage roots and developing shoots. Formation of new adventitious roots at the bud basis is visible. March 2009, Israel.

et al. 1997). Forty primers were screened; 11 of these produced 99 reproducible amplification DNA fragments, useful as polymorphic markers. With these markers, 21 genotypes were distinguished and the similarity values among the genotypes calculated. A dendrogram by cluster analysis revealed that cultivars of *P. lactiflora* were clearly separated from *P. officinalis*, *P. peregrina*, and *P. tenuifolia*. Except for a few cultivars, those of *P. lactiflora* can be broadly divided into Japanese, Chinese and Western groups. Similarly, Guo *et al*. (2011) successfully used sequence related amplified polymorphism (SRAP) to characterize and differentiate 13 cultivars of *P. lactiflora*. Recently, microsatellite (simple sequence repeat, SSR) primers were developed for the *P. lactiflora*, to investigate the diversity within Chinese peony germplasm resources (Li *et al*. 2011). The set of 10 SSRs enlarged the bank of molecular markers available for the herbaceous species of *Paeonia* useful for evaluating genetic diversity, analyzing parentage, identifying hybrids, conserving germplasm, and breeding for desired traits.

PEONY VARIETIES AND HYBRIDS

Herbaceous peony varieties are primarily derived from *P. lactiflora*, "Chinese Peony", native to northeast Asia (Bailey 1916; Everett 1981; Rogers 1995). The majority of these varieties were raised by French breeders in the 19^{th} century, and were well suited to the European climate. After the First World War, the breeding of interspecific hybrids began in the USA, with the intention of lengthening the flowering period and increasing the color range. The number of peony cultivars is estimated to be around 5,000, but many of them are no longer cultivated. For example, most of the cultivars of *P. officinalis*, popular in Europe in the 18^{th} century, were replaced by modern varieties derived from *P. lactiflora* (Page 1997).

The intersectional hybrid peonies (so-called Itoh hybrids) are of particular interest. They were bred by Japanese breeder Toichi Itoh using pollen of tree peony *P. suffruticosa* 'Alice Harding' on the white, semi-double herbaceous peony 'Kakoden'. This cross produced 36 seeds and the first flowers were obtained in 1963 (Smith 2004). The resultant plants had herbaceous stems with tree-peony-like leaves, and pure bright yellow flowers. The color yellow is not found in herbaceous species, but is frequently seen in tree peonies. The American nurserymen Louis Smirnow published the first description of this work in the Bulletin of the American Peony Society in 1967; the same year that four yellow and two pink herbaceous hybrids were registered and thus, the dream of many peony amateurs and producers was accomplished (Smith 2004). The original hybrids have been lost, but were re-created later by several breeders. New genetic combinations yielded an assortment of new shapes and colors. Currently, propagation of these varieties is still challenging, but several biotechnological companies have reported on successful propagation of new intersectional hybrids.

Lists of herbaceous cultivars have been published in a number of books, e.g. "The Gardener Guide to Growing Peonies" by M. Page (1997), "Peonies" by A. Rogers (2000) and "Peonies" by P. McGeorge (2006), as well as in many professional and amateur Internet sites (The Wisconsin Peony Society, www.wipeonysociety.org; American Peony Society, americanpeonysociety.org; The Canadian Peony Society, www.peony.ca; La Pivoinerie D'Aoust Peony Nursery, www.paeonia.com).

Valuable information on local varieties and growth and local production techniques exists in Russian, Spanish, Chinese and Japanese literature, but, unfortunately, this information is less available. Certainly, an international effort is needed to evaluate and summarize these data, as performed by Ji *et al*. (2012), Saez Molina (2012) and Shen *et al*. (2012).

MORPHOLOGICAL STRUCTURE

Peonies grow from an underground crown (tuberous compressed underground stem) and have two types of roots: bulky storage roots and thin fibrous roots (Kapinos and Dubrov 1993). In some species (i.e. *P. officinalis*) roots are able to produce adventitious buds, while in other species (i.e. *P. tenuifolia*) large clumps are formed using underground stolons. Bushy plants are green (**Fig. 1A**), with pink, green or red annual stems that grow to 50-100 cm tall, and leaf shape varies from broad to grass-like. After the flowering season, underground buds (also called "eyes") develop on the crown at the base of the annual herbaceous stems (**Fig. 1C**). These new buds are protected by several sheaths and produce new stems the following spring. Bud emergence begins in spring (**Fig. 1D**). Stems elongate rapidly and reach final heights in 60 to 70 days. Under natural conditions, in the Northern Hemisphere, flowering

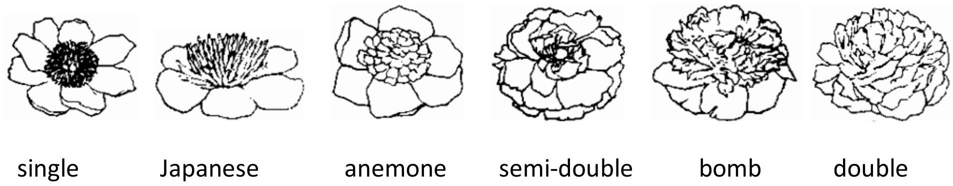

Fig. 2 Flower types in herbaceous peony. • Single peonies have five or more broad petals in one or two rows surrounding a center of golden, pollen-bearing stamens. • Japanese peonies have five or more petals and a center of narrow petaloids or feathery structures called staminodes. The partially transformed stamens may carry a trace of pollen, but are usually not pollen bearing. • Anemone peonies are distinguished by the absence of anthers, while the filaments of the stamens are transformed into narrow and incurved petal-like structures. • Semi-double peonies have five or more outer petals and a center of broad petals intermixed with pollen-bearing stamens. The pollen bearing anthers can be seen while the flower is in bloom. • Bomb peonies have a row of outer guard petals surrounding a pompon tuft of dense petals. • Double peonies have five or more outer petals, the central stamens and carpels are transformed into petals that make up the main body of the large, full flower.

begins in April and continues until the end of June, depending on the location and cultivar. After flowering, the leafy stems remain green until September to October, when the leaves senesce and the peony plants enter dormancy for 3-4 months (Barzilay *et al*. 2002).

Most species have a single terminal flower, although *P. emodi*, *P. veichii* and *P. lactiflora* produce one to three lateral flower buds per stem. Wild peonies typically have five green and persistent sepals and five to ten petals, and close at night or when the sky is very overcast (Page 1997). The number of pistils varies from one to eight, depending on the species, with stamens numbering up to 140. The seed pods are fleshy, and become leathery or woody as they mature.

The breeding and selection process has resulted in a substantial increase of flower forms and colors. Peony types are characterized according to the petal morphology: single, Japanese, anemone, semi-double, bomb and double (**Fig. 2**). All types are grown as cut flowers, though the double types are the most popular, due to the longer postharvest life. Flower colors are white, yellow, cream, pink, rose and deep red.

PLANT DEVELOPMENT AND ANNUAL CYCLE

Seed germination and juvenile period

Peony seeds are brown to black, smooth, and relatively large. During seed development, two types of embryos form successively: the sexual embryo is created by the sexual process (syngamy) and the somatic embryo by the formation of an initial embryoid cell from a somatic cell of the protoderm in the sexual embryo (Batygina and Vasilyeva 2003). Most herbaceous peony species have hypogeal seed germination, when the cotyledons of the germinating seed remain non-photosynthetic below ground. Epigeal germination, when cotyledon expands and becomes photosynthetic above the ground, has only been described for *P. tenuifolia* (Saunders and Stebbins 1938). Under natural conditions, seeds of many species germinate only in the second year due to an underdeveloped embryo, but sometimes sprouting of peony seedlings may take up to five to seven years (Halda *et al.* 2004).

Peony seeds display complex dormancy patterns, in which various parts of the embryonic axis differ in the depth of dormancy. In this case, radicle emergence occurs readily, but the epicotyl requires specific growing conditions (Bewley and Black 1994). Similar to many other species from temperate regions (e.g., *Trillium*, *Allium tricoccum*, and *Hepatica*), peony seeds have deep, simple epicotyl morphophysiological dormancy. The epicotyl appears to be sensitive to cold stratification, only after the radicle has elongated (Baskin and Baskin 2001). For root emergence, a relatively high temperature of ~20°C in the dark is required. Following primary root emergence, dormancy release of the cotyledon leaf requires one to four months of low temperatures. Leaf sprouting and elongation occur when temperatures increase to 15 to 20°C after the cold period (Baskin and Baskin 2001).

Under experimental conditions, epicotyl dormancy was broken in *P. lactiflora* embryos after topical application of agarose gels containing gibberellic acid (GA_3) and 6-benzylaminopurine (BA). Cultivation of isolated embryos significantly increased dormancy release and leaf formation (Buchheim *et al*. 1994). Similar results were recently shown for the seeds of Chinese cultivars. BA and GA_3 had a positive effect on promoting germination and embryo growth, while addition of 0.5 mg/L α-naphthaleneacetic acid (NAA) to the culture medium significantly enhanced rooting (Gao 2010). Axillary buds can be induced in peony seedlings by adding GA_3 (1.84 mg/L), sucrose (11.02 g/L) and glucose (17.13 g/L) to the *in vitro* culture medium (Yu *et al*. 2008).

The juvenile period of herbaceous peonies lasts for 3 to 5 years, and in some species first flowering was observed only after 6 to 7 years of vegetative growth (Uspenskaya 2002). However, the possibility of shortening the juvenile stage by environmental manipulations was recently reported (Jacob *et al*. 2006). In the first growing cycles, duration of the controlled cold treatment was only about 2 weeks, as compared with 6 to 8 weeks required for dormancy release of the adult plants. This approach allowed several developmental cycles during one calendar year. Consequently, first flowering of peony seedlings was obtain less than 27 months after seed sowing (Jacob *et al*. 2006).

Annual developmental program

Annual development of herbaceous peonies is similar to that of geophytes that originate from regions with cold win-

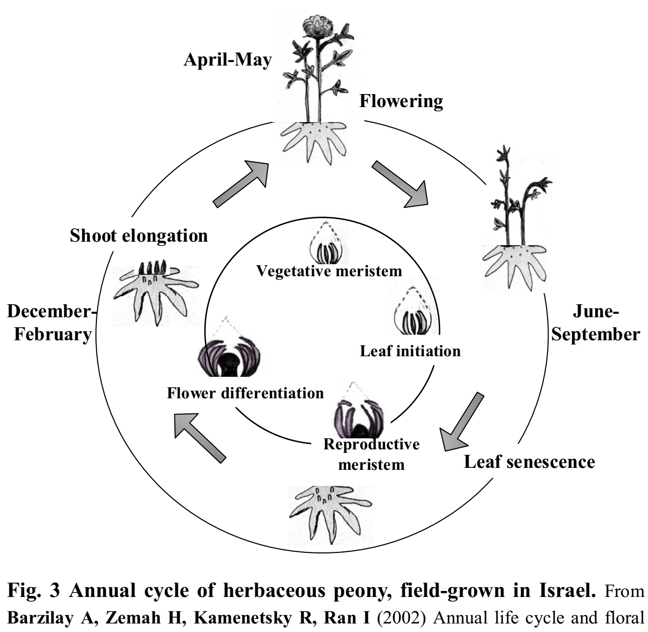

Fig. 3 Annual cycle of herbaceous peony, field-grown in Israel. From **Barzilay A, Zemah H, Kamenetsky R, Ran I** (2002) Annual life cycle and floral development of 'Sarah Bernhardt' peony in Israel. *HortScience* **37**, 300-303, ©2002, with kind permission from ASHS, Alexandria.

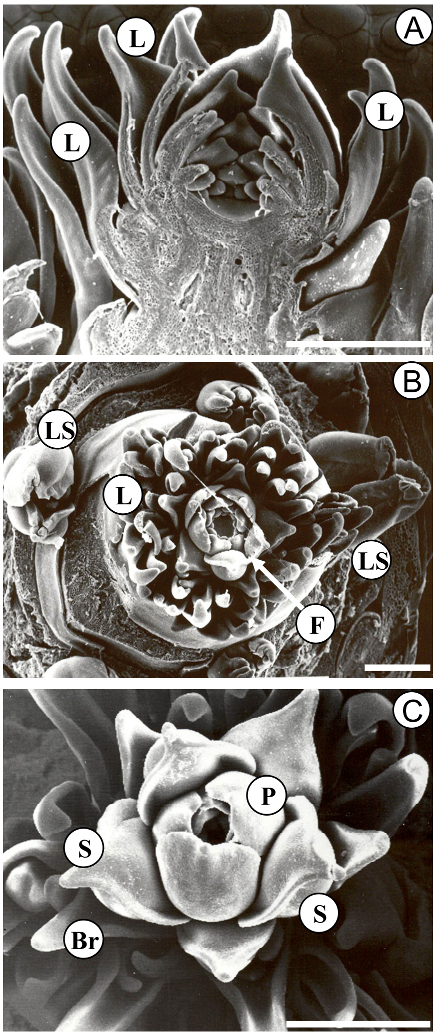

Fig. 4 Scanning electron microphotographs of intrabud development of *Paeonia* 'Sarah Bernhardt' in Israel. (**A**) Initiation of leaf primordia (L) in the apical meristem in June. Flat apical meristem is visible in the central part of the bud. Bar = 0.5 mm. (**B**) Floral differentiation in November. Leaf primordia (L) surround the developing flower (F). Petal differentiation begins on the periphery of the generative meristem and progresses centripetally. In addition to the central flowering shoot, each renewal bud contains 3-6 axillary lateral shoots (LS). Cover leaves removed. Bar = 1 mm. (**C**) After formation of sepals (S), numerous petals (P) and petaloids, differentiation ceases at the beginning of December. An undifferentiated space 0.5-0.7 mm in diameter remains between central petals (P) of the developing flower. Bar = 5 mm. From **Barzilay A, Zemah H, Kamenetsky R, Ran I** (2002) Annual life cycle and floral development of 'Sarah Bernhardt' peony in Israel. *HortScience* 37, 300-303, ©2002, with kind permission from ASHS, Alexandria.

ters and dry, hot summers (Flaishman and Kamenetsky 2006; Walton *et al.* 2007), as well as deciduous fruit trees (Erez *et al.* 1988; Kamenetsky *et al.* 2003). Plants flower in the spring, initiate subsequent flowers during the summer, and shed their leaves and enter dormancy in late autumn.

Once the peony plant reaches the flowering stage, the annual cycle of the adult plant is regulated by environmental conditions (Evans *et al.* 1990). The annual life cycle of field-grown peony 'Sarah Bernhardt' was studied in detail under local conditions in Israel (Barzilay *et al.* 2002). Renewal buds of various sizes develop on the underground crown at the base of the annual herbaceous stems after spring flowering. The large buds will produce new stems the following spring, while the smaller buds will remain dormant until the next season, or will produce only small sprouts. Under Israeli conditions, the new monocarpic shoots are initiated in the renewal buds, with the formation of the first leaf primordia at the end of June, and continue to increase in size until February (**Fig. 3**). During the summer, the renewal buds contain only vegetative meristems. The apical meristem ceases leaf formation during senescence of the aboveground shoots in the fall. During September, the apical meristem of the renewal buds reaches the generative stage and achieves the form of a dome, but remains undifferentiated (**Fig. 4**). In October, the floral parts become visible. Floral differentiation is completed by the beginning of December (**Fig. 4C**). Differentiation of the peony bud includes formation of bracts, calyx, petals, stamens and pistil (Huang *et al.* 2009).

The factors inducing leaf abscission, bud dormancy and flower formation of peonies are unknown. According to Wilkins and Halevy (1985), flower initiation in peonies is autonomous i.e. proceeding without the need for an external temperature or photoperiod signal. This hypothesis still needs an experimental confirmation.

Reproduction and resource allocation to male and female functions in *P. officinalis* was studied during two reproductive seasons in relation to plant size (Andrieu *et al.* 2007). It was shown that large plants allocated more resources to reproduction by the production of additional flowering stems. However, in terms of relative allocation, large and small plants allocated a similar proportion of resources to reproduction. *P. officinalis* is a hermaphroditic plant, but gender modification is size-dependent, and larger plants produce more female flowers than small plants.

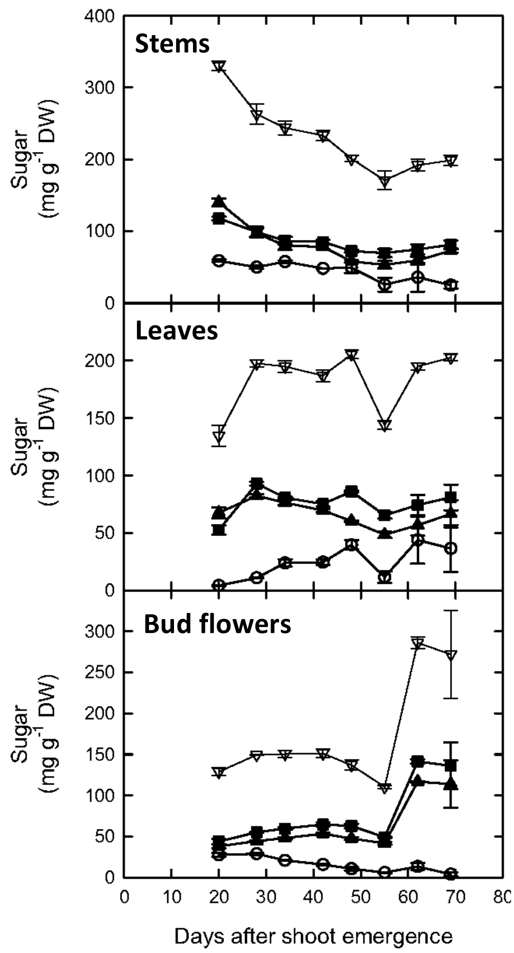

Fig. 5 Changes in the concentration of individual sugars. Fructose (square), glucose (full triangle), sucrose (circle) and total sugar (empty triangle) concentration during floral shoot development in peony stems, leaves and bud flowers. Bars = ±SE. Adapted from **Walton EF, McLaren GF, Boldingh L** (2007) Seasonal patterns of starch and sugar accumulation in herbaceous peony (*Paeonia lactiflora* Pall.). *Journal of Horticultural Science and Biotechnology* **82**, 365-370, ©2007, with kind permission from the Editor.

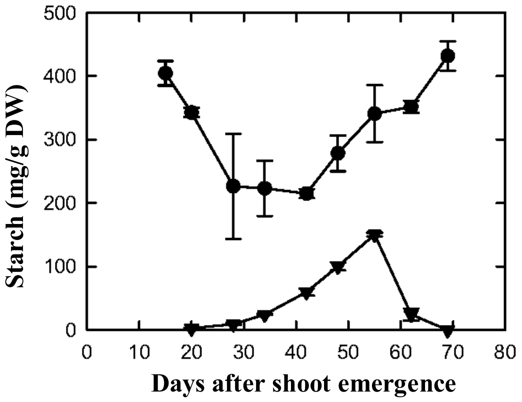

Fig. 6 Changes in starch concentration in peony roots (circles) and in bud/flowers (triangles) during floral shoot development from shoot emergence until after flower opening. Bars=±SE. Adapted from **Walton EF, McLaren GF, Boldingh L** (2007) Seasonal patterns of starch and sugar accumulation in herbaceous peony (*Paeonia lactiflora* Pall.). *Journal of Horticultural Science and Biotechnology* **82**, 365-370, ©2007, with kind permission from the Editor.

Physiological and biochemical aspects of annual plant development

1. Resource allocation

Peonies are deciduous and winter-dormant, and the carbon required for dormancy release and initial growth in the spring is supplied from reserves accumulated in the storage roots (Walton *et al.* 2007). The major sugars detected in peony plants are fructose, glucose, sucrose and *myo*-inositol, and the main storage carbohydrate is starch (**Fig. 5**). Starch concentrations in the roots decline with the resumption of growth in spring, and begin to increase after shoot emergence and throughout flowering until mid-summer (**Fig. 6**). The ability to accumulate starch reserves in the roots during stem growth and flowering provides a significant adaptive advantage for peonies, allowing them to survive in various climates, particularly in environments with short growing seasons (Walton *et al.* 2007). Similar to many other geophyte species (e.g., *Lilium* and *Alstroemeria*), flower buds of peony accumulate starch prior to flowering. Initial starch hydrolysis coincides with a general loosening of the tightly furled buds, whereas the rapid hydrolysis occurs during the final stages of flower opening. This mechanism allows slow (5 to 6 days) opening of flower bud prior to anthesis (see also section **Postharvest**).

Seven stages of plant development were revealed from dormancy release to anthesis (Cheng *et al.* 2009b). During plant growth, temperature regime affects stem elongation and flower development. Inappropriate temperature regimes can cause too slow or too fast stem elongation or flower abortion, and result in the absence of flowering or in poor flower quality. Precise temperature studies provide the scientific basis for development of forcing protocols to extend the harvest period for various peony cultivars and to reach the highest prices for out-of-season cut flower production.

2. Chilling requirements for dormancy release and stem elongation

In late autumn above-ground peony shoots senesce and die. The dormancy of the underground buds is broken by exposure to low temperature, which allows them to emerge and grow in the spring (Kamenetsky *et al.* 2000, 2003). In field grown peony plants, the chilling requirements for dormancy release were determined by exposing plants to ambient winter-cold weather in Northern Israel (8-10°C night, 16-26°C day, average *ca.* 17°C from November to February) (Halevy *et al.* 2002). Following the accumulation of chilling units, the greenhouses were covered with plastic sheets at different dates. The accumulated chilling units were calculated according to Fishman *et al.* (1987) and Erez *et al.* (1988). Flowering occurred two months after dormancy release.

When container grown plants of ‘Sarah Bernhardt’ were cooled artificially, dormancy release was found to be best under chilling regimes of 2°C for 60 days or 6°C for 70 days (Kamenetsky *et al.* 2003). Warmer temperatures were less effective. Comparison of the sprouting of plants exposed to 2, 6 or 10°C for 60 days clearly indicates that the chilling effect on dormancy breaking intensified as the chilling temperature was lowered. The effect was more pronounced on the number of sprouting stems than on the stem length. It should be noted, however, that low temperatures (~ 0°C) enhanced dormancy release of many renewal buds, but caused flower abortion, probably due to the resource allocation and intense vegetative growth at the expense of the reproductive organs (Kamenetsky *et al.* 2000)

In New Zealand, potted plants of early flowering ‘Coral Sunset’, mid-season flowering ‘Monsieur Jules Elie’, and late flowering ‘Sarah Bernhardt’ were stored at 1, 4, or 7°C for different durations (3, 6, 9, or 12 weeks) to determine their chilling requirements for flower production (Fulton *et al.* 2001). Control plants were forced without chilling and produced no shoots or flowers. Chilling was followed by forcing at 18°C in a controlled greenhouse until flowering had finished. For all cultivars, the mean number of shoots and flowers increased as plants were subjected to colder chilling temperatures, or longer chilling durations. However, after 9 weeks of chilling no significant within-cultivar differences were registered between different temperature regimes. The time to sprouting after the completion of chilling treatments consistently decreased as the duration of the chilling treatment increased. Although one could expect that the earliest flowering types would require the least amount of chilling, the authors suggest that the early flowering ‘Coral Sunset’ required the greatest amount of chilling to sprout consistently, while ‘Sarah Bernhardt’, a very late flowering type, required the least. The mid-season cultivar ‘Monsieur Jules Elie’ needed significantly more chilling than the other two cultivars to achieve maximum flowering potential (Fulton *et al.* 2001). Therefore, sprouting and flowering potential of peonies depends on temperature regime and duration of chilling period, while earliness or lateness appears to be a genetic trait that is not regulated by temperature.

Application of GA_3 to dormant underground buds can partially substitute the cold requirement for breaking dormancy and promote bud sprouting and shoot growth (Evans *et al.* 1990; Halevy *et al.* 2002). GA_3 treatment does not promote flower initiation and differentiation in peonies, and is not effective if applied before flower formation (Halevy *et al.* 1995). Observations on 20 Chinese varieties under ambient and forcing conditions concluded that only five of them were suitable for forcing (Cheng *et al.* 2009b). In ‘Da Fu Gui’, chilling promoted dormancy release and plant growth. Stem height, flower size and flowering rate were positively affected by both chilling and spraying with 200 or 500 mg/L GA_3, while leaf extension (maximum width of foliage) was influenced only by GA_3 (Cheng *et al.* 2009b).

Halevy *et al.* (2002) suggested that photoperiod does not affect flower formation and stem elongation in herbaceous peonies. Recently, this assumption was supported by Niu *et al.* (2010). Illumination of two *P. lactiflora* cultivars for 8, 10, 12 and 14 h per day did not affect growth rhythm and flowering period, but significantly influenced quality of cut flowers. Shorter photoperiod was beneficial for one variety ('Taohuafeixue'), while 14-h day length enhanced flower quality in the second variety ('Zifengyu'). The effect of photoperiod, light intensity and light quality should be addressed in future research to optimize pre- and post-harvest quality of cut flowers.

Fig. 7 Flower abortion in early (A) and late (B) stages of floral development of peony 'Sarah Bernhardt' and normal flower bud (C). From **Kamenetsky R, Barzilay A, Erez A, Halevy AH** (2003) Temperature requirements for floral development of herbaceous peony cv. 'Sarah Bernhardt'. *Scientia Horticulturae* **97**, 309-320, ©2003, with kind permission from Elsevier, Amsterdam.

3. Effects of growth temperatures on plant development

Following the fulfillment of chilling requirements, growth temperatures significantly affect the dynamics of bud emergence, stem elongation and anthesis in herbaceous peony. In recent experiments, the container-grown pre-chilled plants of 'Sarah Bernhardt' were exposed to three temperature regimes: 16/5, 22/10 or 28/10°C (day/night, respectively) (Kamenetsky *et al.* 2003). At low temperatures, bud emergence was slow and the elongation of the first stems was observed only at 50 days. The stems reached a length of 55 cm after 85 days of growth at 16/5°C. Flower quality in this treatment was, however, better than that of plants grown at higher temperatures: the stems were stronger and the flower color was more intense. Production temperatures of 22/10°C resulted in rapid sprouting of the stems and an average stem length of 85 cm. Bud emergence was fastest at 28/10°C, the maximum number of shoots was observed after only 36 days of growth.

Growing temperatures significantly affected the flowering date. Anthesis occurred after 50 to 60 days at high temperatures, even when the plants were initially exposed to 22/10°C for 30 days and were subsequently transferred to high temperatures. Continuous growing at 22/10°C led to flowering after 83 days. Maximal realization of flowering potential was achieved at growing temperatures of 22/10°C (Kamenetsky *et al.* 2003).

In New Zealand, pre-chilled potted plants of 'Coral Sunset', 'Monsieur Jules Elie', 'Sarah Bernhardt', and 'Karl Rosenfeld' were forced in a range of controlled temperature regimes (Hall *et al.* 2007). For all cultivars, warm temperatures of up to 25°C led to more rapid shoot emergence and flower development. The rate of development from shoot emergence to flower opening increased linearly with warmer temperatures. Cultivars varied in the number of heat units required for shoot emergence. 'Coral Sunset' shoots were the first to emerge and last to emerge was 'Monsieur Jules Elie', which took 50% longer to emerge than 'Coral Sunset'. No significant differences were found among cultivars in the time taken from shoot emergence to flower opening, although the stage of bud opening was slightly earlier in 'Karl Rosenfeld' (Hall *et al.* 2007).

4. High growth temperatures cause flower abortion

Recent attempts of peony production in warm regions posed new questions on the effect of high growth temperatures on flower development and cut flower quality. It was shown that under sustained high day and night temperatures of 28/22°C, almost all stems aborted their flower buds, mostly during the early stages of flower development. The transfer of the plants from 22/10°C to 28/22°C after 30 days of growing also caused abortion of most flower buds (**Fig. 7**). In contrast, when plants were grown for the first month at 28/10°C and then transferred to 22/10°C, flowering was not significantly different from that of plants grown continuously at 22/10°C (Kamenetsky *et al.* 2003). However, exposure to higher night temperatures of 22°C during the first 20 days of growing caused a very high abortion rate of young flower buds. In these controlled condition experiments, the temperature regime of 22/10°C (day/night) was found to be optimal for the production of quality flower stems and proper flower development.

Of course, under natural growing conditions, large temperature variations are common. In order to expand cut peony production, biological limitations of the peony will need to be considered. Production techniques should be developed for heating during long and cold springs and for cooling and ventilation when air temperatures are too high to avoid flower abortion and produce strong stems. The same techniques will help prevent foliar diseases, which are caused by high air humidity and excessively high or low production temperatures.

PROPAGATION

Seed propagation

Seed propagation of peonies is not common in commercial production, due to the complicated process of seed germination, the long juvenile period and seedling trait variability that occurs with sexual reproduction. However, commercial and amateur breeders propagate peony by seeds. Slow propagation by seeds makes peony breeding very time consuming, and this fact has contributed to the low commercial interest in peony breeding by large international companies.

Jacob *et al.* (2006) recommended the following protocol for seed germination:

- Place seeds in a moist soil-less substrate in sealed plastic bags
- Store bags at a warm temperature (~ 20°C) in the dark for one month.
- Sow seeds with an emerged root in pots containing a mixture of peat and perlite and place in a greenhouse for one month.
- Place the pots in a dark, cold room (4°C) for 15 to 30 days to stimulate aerial growth.
- After the first leaf develops, place the pots under greenhouse conditions (15-25°C, depending on the season, which corresponds to the normal temperature of plant development.

Many seed germination protocols for different herbaceous peony species and hybrids can be found via Internet sources (www.peony.ca; www.paeonia.com). Most of them recommend warm-cold cycle for dormancy release, followed by a transfer to pots and growing under light conditions. Many sources recommend a prolonged period (up to four months) of cold for shoot emergence.

In regions with a temperate climate and cold winters, seeds can be sown directly in the ground. In this case, the above-ground shoots might appear only in the second spring, since a mature seed with a hard seed coat is not able to overcome the first dormancy in the fall and to develop a primary root. Therefore, the seed remains in the soil until the following spring, when the warm moist conditions allow release from the first dormancy. Then the seed overwinters again to overcome the second dormancy before producing a shoot in the following spring (La Pivoinerie D'Aoust Peony

Nursery, www.paeonia.com).

As previously mentioned, the juvenile period might last for 4 to 6 years, and the first flowers are not always indicative of a plant's potential. It may well be 7 years before a mature, stable flower is obtained.

Vegetative propagation

Vegetative propagation is the most reliable propagation method in commercial production, as well as in private gardening.

1. Crown division

Crown division is the most popular technique used to propagate herbaceous and Itoh peonies. For successful propagation in moderate climate regions, it is recommended to cut back the peony foliage in late summer or early autumn, and to dig the plant up with an intact crown and as much of the root system as possible. After washing the roots, the plants should be left in the shade for several hours. Crown divisions must have at least one visible crown bud to grow; however, three to five buds per division produce stronger and healthier plants. The new divisions can be stored in peat moss filled bags for several days as long as they are not subject to large temperature variations (La Pivoinerie D'Aoust Peony Nursery, www.paeonia.com). In Dutch commercial production, peony growers divide the crowns after harvest in October to November and store them outside until the shipment of plant material in January to March.

2. Renewal buds with small crown segment

This technique is similar to crown division. After harvest in late summer, the crown is divided into many small fragments, each containing a renewal bud with a small crown part (Ippolitova 2009). These propagation units are planted 3 to 4 cm deep in beds with a light, well-drained substrate, where constant humidity can be maintained. During dry and warm periods, propagation beds should be shaded. During cold winters, plants need to be protected by mulch, which has to be removed prior to sprouting in spring. After one year, new and well-developed plants can be replanted in a permanent plot. Uspenskaya (2002) recommends this method for the re-juvenation of plant material and mass-propagation of rare varieties.

3. Green shoot cuttings

This method was described in Russian literature (Kapinos and Dubrov 1993; Uspenskaya 2002) and has a relatively low success rate (15-20%). However, this method can be used when the breeder or producer does not want to damage the crown of the mother plant, or when propagating very rare varieties. Unfortunately, this method is not suitable for many hybrids.

Shoot cuttings are harvested two weeks before flowering. Only one-third of the shoots can be removed from an adult plant. Each shoot produces two to three cuttings, containing two leaves and one internode. The lower leaf should be removed, while two thirds of the upper leaf should be cut and removed in order to decrease transpiration. The best rooting was obtained from cuttings taken from the lower part of the stem, located closer to the crown. To increase rooting, cuttings can be treated with indole-3-acetic acid (IAA) or NAA (5-10 mg/L) for 12 to 24 h and then rinsed in water prior to planting. The rinsed cuttings should be planted in vermiculite or a well-drained substrate, with the lower node inserted to a depth of 3 to 4 cm and cuttings spaced 10 to 20 cm apart to avoid diseases and rotting of the plants. Optimal air and substrate temperature for rooting is 20 to 25°C, with a relative humidity of 90 to 95%. Using fog can increase the rooting percentage, but also increases disease and rotting of the cuttings. During the first two weeks, cuttings should be shaded and preventatively sprayed with fungicides. Callus tissue is formed after 3 weeks and rooting is visible after 1.5 to 2 months (Ippolitova 2009).

Even after successful rooting, the critical stage of cutting development is the further formation of the renewal bud in the lower node. If this bud does not form, the plant will die, even if it has developed a root system. In cold regions, rooted cuttings should be protected during the first winter. In the case of successful rooting and bud formation, new plants will flower after three to four years of growth and development.

4. Root cuttings

This method was proposed for the hybrids of *P. officinalis*, *P. peregrine* and *P. tenuifolia,* which are able to form renewal buds on storage roots (Rogers 1995). Rubinina (2009) suggests that some hybrids (e.g., 'Carol', 'Henry Bockstoce', 'Ellen Cowley') can be propagated using this method. However, most *P. lactiflora* hybrids do not produce buds on adventitious roots.

For propagation, storage roots can be divided during autumn into 1 to 3 cm long sections, treated with fungicides and planted in 5 to 6 cm deep boxes filled with clean river sand. Boxes should be stored at ambient temperatures or at 3 to 8°C in cold regions to protect cuttings from frost. During winter, the sand should be slightly moist. The renewal buds begin to form in February or March, and new shoots will sprout with increasing temperature (April-May in the regions with moderate climate). New plants should be protected from high and low temperatures, and can be re-planted in a permanent plot after 3 years (Kapinos and Dubrov 1993; Uspenskaya 2002).

5. Layering

Layering is a technique in which a section of the stem is manipulated to develop roots while still attached to the mother plant. This method has been described for tree peonies (Rogers 1995), but in Russian literature it is called "Chinese techniques" and was also proposed for herbaceous peony species (Uspenskaya 2002). In early spring, as buds begin to sprout, they should be gently exposed and covered with a well-drained mixture of sand and compost, with an addition of 300 to 400 g of bone meal and 150 g superphosphate per plant. Thereafter, the plant is covered by a 50 × 50 cm frame that is 40 cm high. When the shoots first sprout, the frame should be filled with a sand/compost substrate of up to 10 cm. As the stems elongate, the substrate should be raised to 25 to 30 cm. Regular watering is necessary for successful rooting. At the end of the next season (late summer), the frames can be removed, and the rooted shoots can be separated from the mother plants and re-planted to a nursery. This procedure can be repeated using the same plant only once in 3 to 4 years.

6. Micropropagation

Tissue culture is the practice of producing a large number of progeny plants when vegetative reproduction is slow or difficult. This method is often used to propagate novel plants and/or to provide a large number of plantlets from stock plants. The development of fast, reliable tissue culture protocols would facilitate the rapid introduction of new varieties into commercial markets. Research groups in the USA, China, Japan and Poland have reported successful multiplication of peony *in vitro*, and several commercial companies are already using micropropagation for propagating rare varieties. A procedure for *in vitro* propagation of 'Takinoyosooi' and 'Sarah Bernhardt' through shoot tip culture was described by Hosoki *et al.* (1989). Half strength Murashige-Skoog medium, supplemented with 6-BA and GA, promoted formation and growth of axillary buds. Continuous shoot multiplication was achieved by vertically

Table 2 List of the common peony diseases (adapted from: Stevens *et al.* 1993)

Disease	Pathogen	Symptoms
Blights and Leaf spots	*Botrytis* spp.	Blight. Sudden wilting of shoots. Brown or black rot can be seen at the base of stems, below ground. Grayish fungal growth is visible on stems just above soil line. Infected flowers turn brown, and large, irregular, brown areas develop on leaves. Fungal growth may also develop on infected plant parts.
	Pytophtora cactorum	
	Cladosporium spp.	
	Cercospora paeoniae	
	Phyllosticta spp.	Red spot or measles. Small, dark red, circular spots on leaves. Spots coalesce to form blotches that are dark purple on lower leaf surface.
	Septoria paeoniae	
Rots and Wilts	*Verticillium albo-atrum*	During the flowering period, foliage and shoots may wilt, with the lower shoot remaining intact. An internal vascular discoloration may be present in the lower stem.
	Fusarium spp.	
	Rhizoctonia solani	
	Schlerotinia schlerotiorum	Several soilborne fungi may damage the roots and crowns of peony. Roots and crowns may exhibit brown to black lesions.
	Thielaviopsis basicola	
Root nematodes	*Meloidogyne* spp.	Plants are stunted and spindly and fail to bloom. Roots have numerous small galls
	Rotylenchus buxophilus	
Virus	Peony ringspot	Greenish-yellow concentric bands, occasionally small, necrotic spots

splitting the shoot axis and the subsequent division of elongated axillary shoots every 36 days. High rooting frequency (57-100%) was obtained on paper-bridge liquid medium supplemented with Indole-3-butyric acid (IBA). Half of the rooted plantlets were established on porous substrate. Thus, it was suggested that 300 to 700 plants could be obtained from a single bud during one year.

For dormant bud explants, the most successful sterilizing procedure was soaking in 0.1% aqueous mercuric chloride for 10 min (Zhang *et al.* 2006). The addition of 3.1 mg/L GA and 1 mg/L BA was recommended for bud induction; multiplication and root induction were enhance by 1 mg/L BA + 0.5 mg/L kinetin (KT) and 1 mg/L IBA, respectively.

Tian *et al.* (2010) investigated the shoot induction ability of explants. Callus was readily induced from stem and petiole explants within 2 days of culture, but failed to generate shoots. Adventitious shoots were successfully produced from meristematic regions only: underground buds on nodal stem sections, petioles and petiolules. Sections containing nodal junctions were the most effective explants. Thidiazuron (TDZ) was more effective than BA at inducing shoots, and a 100% shoot induction rate was obtained in medium containing 0.1–3 mg/L of TDZ. However, higher concentrations of TDZ inhibited shoot elongation and only large leaf clusters were produced. GA_3 was beneficial for shoot and stem elongation (Tian *et al.* 2010).

The Polish group of Gabryszewska (2001, 2006) developed techniques for peony multiplication in tissue culture and showed that temperature had a significant effect on peony multiplication. Chilling peony shoots at +4°C for two months activated further growth and development of the shoots. The cooled explants, subsequently grown at 15°C, produced the highest numbers of shoots and leaves during the first subculture. Dormancy was induced along with reduced growth and multiplication rates and leaf senescence in shoots propagated under a constant high temperature (20-25°C) (Gabryszewska 2006). The physiological state of the explants (dormant vs. non-dormant shoots) of 'Jadwiga' influenced the reaction of the explants to the application of plant hormones or light conditions (Gabryszewska 2001). In dormant shoots, growth and multiplication rates were reduced. The application of abscisic acid (ABA) or fluridone to the cytokinin-free medium had no effect on the number of axillary shoots, but influenced the leaf formation on non-dormant and dormant shoots. The highest number of leaves and shoots were found on explants grown under red light, both on non-dormant and dormant shoots.

The rooting *in vitro* and acclimatization in a greenhouse were investigated using 'Jadwiga' and 'Professor Wojcicki' (Gabryszewska and Kawa-Miszczak 2010). The presence in the medium of auxins (IBA 1 mg/L + IAA 1 mg/L + 0.01 mg/L NAA) and 30 g/L of sucrose stimulated the number of roots/shoot. At the same time, a higher rooting percentage was found using the auxin-free medium in the presence of high level of sucrose. The two cultivars varied in acclimatization potential and temperature requirements for rooting. After four weeks of greenhouse acclimatization, the plantlets accumulated starch, showed strong inhibition of shoot growth, and developed dormant buds.

A comprehensive review of micropropagation of herbaceous peony (*P. lactiflora*) was recently published by Shen *et al*. (2012). This valuable review comprehensively covers advances made in various aspects of tissue culture and micropropagation, especially published in Chinese.

DISEASE CONTROL

Diseases often reduce the quantity and quality of peony flowers and, in some cases, cause significant plant mortality. Some diseases, such as botrytis blight and red spot, are perennial, while others may be sporadic. Peony diseases can be controlled by a combination of cultural management and chemicals. It is recommended to start commercial production with clean, high-quality plant material, and to treat the propagation units and roots with a fungicide dust before direct planting in the field (**Table 2**; Stevens *et al.* 1993). Overhead watering, poor air circulation and overcrowding may cause plant losses from red spot and other fungal and foliar blights.

The major disease that seriously threatens peonies is botrytis bud blight, caused mainly by *Botrytis paeoniae* and *B. cinerea* (Rogers 1995; Page 1997). It can be controlled by regular spraying with a systemic fungicide and the removal and destruction of dead foliage at the end of the season. Control is much more effective if the fungicides are applied before symptoms of red spot are apparent. Other fungal diseases may be controlled by curative fungicide applications beginning as soon as symptoms develop.

Viral disease of peony, which is associated with strains of *Tobacco rattle virus* (TRV) and known as peony ring spot disease, has been reported worldwide (Europe, United States, Japan, and New Zealand) for several years (Chang *et al.* 1976; Robertson *et al.* 2009; Samuitienė *et al*. 2009). In addition, *Alfalfa mosaic virus* (AMV) was recently identified in plants cultivated at the Botanical Garden of the University of Parma, Italy (Bellardi *et al.* 2003), and *Cucumber mosaic virus* (CMV) was found in *P. lactiflora* in France (Cardin *et al.* 2010).

HARVEST, POSTHARVEST AND TRANSPORTATION

Propagation material

Postharvest information is categorized into the handling of dormant propagation material and of cut flowers. Dormant crowns are harvested in late summer or fall, after the shoots have senesced naturally for winter dormancy. Large clumps can be cut into sections with three to five growing eyes and graded. In addition, the crowns may be subjected to a hot water bath to prevent or cure nematode infestations. The crowns are treated for 2 h at 43.5°C for prevention and for one hour at 45°C if contamination is likely (P. Wierstra, personal communication). Such treatment should occur as soon as possible after the digging of the crowns. Crowns for potted plant production are shipped to the finished plant producers soon after harvesting and processing, as the crowns usually form roots in the container before winter.

After grading and processing, the crowns can be stored at 2-3°C until further processed and packaged in early January, in the Northern Hemisphere. Other recommendations call for storing the crowns initially at 15 to 18°C and lowering the temperature gradually until early January. Regardless of previous temperature treatments, in early January the temperature can be dropped to -2°C until the crowns are shipped or planted. Propagation material can be stored until the end of June, although crowns stored until then are generally slower to grow in the first year than those not stored as long.

Cut flowers

Harvest, cut stage and post-harvest treatments. For cut peony stems, the harvest stage is critical as the flowers can open quickly. Consequently, peony stems may need to be harvested up to three times a day if temperatures are warm. Post (1949) recommended harvesting early in the morning, with late evening the second best time. The opening of peony buds is separated into six stages (Gast *et al.* 2001):

1. Tight bud with little true petal color showing
2. Tight bud with true petal color showing
3. Soft bud
4. Very soft bud
5. Almost open with petals not reflexed but still curving inward towards the center
6. Fully open

Needless to say, these stages are quite subjective, requiring the use of well-trained harvesters. In particular, stages 2 to 4 depend on the degree of softness of the bud. The degree of softness for optimum postharvest life varies with the cultivar. In general, white flowered cultivars are the first to open, pinks are intermediate, and red the slowest. The less mature the flower bud, the longer the vase life (Eason *et al.* 2002). Bud development observation by Yu *et al.* (2011) showed great differences in optimum harvesting stage between 11 cultivars, especially between the hybrid peony group and *lactiflora* group. Bud diameter was not be the only indicator that could be used to select optimum harvesting stage and various other parameters were needed including sepal opening angle, sepal color, petal color showing, and degree of firmness. Yu *et al.* (2011) determined that 'Pink Hawaiian Coral', 'Red Charm', 'Edulis Superba', 'Red Magic', and 'Sarah Bernhardt' should be harvested at stage 1. 'Duchesse de Nemours', 'Taff', 'Sorbet' and 'Monsieur Jules Elie' should be harvested at stage 2. 'Kansas' should be at stage 3 and 'Karl Rosenfield' at stage 4.

Postharvest grades and standards have been established (Post 1949). Double, bomb or semi-double flowered peonies are generally more popular than single types, possibly due to the long vase life of the doubles, which have more petals to open.

Ongoing questions for peony postharvest include concerns about when to start harvesting from new plantings, the number of stems that can be harvested from each plant and the amount of foliage to leave when harvesting. Rogers (1995) recommended that all flower buds but one can be removed from the plants the first year to encourage vegetative growth. The one remaining flower is used to confirm the cultivar of the plants. Commercial harvest can commence the third year if only about 30% of the stems are harvested, with full production occurring in the fourth and fifth years. Decker and Weinard (1931) noted that plants produced the most flowers when all the stems were cut, leaving three leaves on each stem. In contrast, fewer stems were harvested annually when they were removed down to the ground. However, allowing leaves to remain on the plant reduced stem length and the subsequent sale price. In contrast, Rogers (1995) noted that 50 to 75% of the stems could be harvested if the two lowest leaves were left on the plant. Longer stems could be harvested if fewer stems were cut from each plant. As noted earlier, an increasing amount of winter cold treatment increases stem length, ranging from 25 cm for stems harvesting in central California, to 45 cm in eastern North Carolina, and 60-90 cm in Wisconsin (Armitage and Laushman 2003).

Stem strength of cut peonies was most highly correlated with stem diameter, but not with fresh weight of cut stems (Zhao *et al.* 2012). Lignin had a significant impact on stem strength, while cellulose was not related to stem strength. Li *et al.* (2012) showed that preharvest sprays with 4% (w/v) calcium chloride applied three times after bud emergence strengthened cut 'Da Fugui' stems. In addition, calcium sprays increased the concentrations of endogenous calcium and total pectin content. Gast (1995, 1996, 1997, 1998, 1999, 2000) conducted annual production and postharvest evaluations from 1992 to 2000 and noted that the vase life of freshly harvested flowers from 28 cultivars ranged from a low of 4.4 days to a high of 8.7 days. Large variations in vase life can occur from one year to the next, however (Gast 1995, 2000). Cheng *et al.* (2009a) grouped 15 Chinese cultivars into either fold-petal or open-top types, which exhibited a different flower morphology during harvest stages 2 through 6. Of 26 garden cultivars tested, Li *et al.* (2009) ranked 6 as suitable for cut flower production, 11 as secondarily suitable, 5 as hardly suitable and 3 as not suitable based on 13 characteristics. The top cultivars were 'Shaonvzhuang' and 'Qingwen', which had vase-lives of 5.2 and 4.6 days, respectively.

Flowers are typically picked early in the morning and stored dry by the grower. It is recommended to cool flowers to 1°C as quickly as possible, and to grade and bunch the stems rapidly without allowing the flowers to warm up. Flowers hydrated by the grower are more likely to open during shipping.

Due to the relatively short flowering season at any one location, there is a strong interest in long-term storage of cut peonies. The season can be extended by long-term cold storage of the flower buds at 0 to 1°C in plastic lined boxes for up to 3 to 4 weeks (Gast 2000; Eason *et al.* 2002). Cut peonies maintained a vase life of 4.7 to 8.6 days, depending on the cultivar, after 4 weeks of storage (Gast 2000). Longer storage of up to 12 weeks is possible, but vase life and flower size will be reduced (Nowak and Rudnicki 1990; Gast 2001; Zang and Lui 2003; Walton *et al.* 2010). Flowers for long term storage are generally not hydrated, to prevent opening and botrytis development during storage; however, some growers hydrate at 0 to 2°C for 1 to 2 h after harvest, then sort, grade and bunch, and allow the foliage to air dry before being packed in boxes for storage.

The role of carbohydrates in the postharvest handling of cut peonies has been examined. Starch is the main storage carbohydrate and the highest levels (58% of total carbohydrates) were attained immediately before flowers open (**Fig. 8**) (Walton *et al.* 2007). Walton *et al.* (2010) documented that during flower opening the rate of starch hydrolysis in the fresh-cut, non-stored flower buds was more rapid than in those still attached to the plant. Not surprisingly, the total sugar concentrations of the flowers, leaves and stems were lower in fresh-cut flowers than in those still attached to the plant. However, the authors estimated that fresh-cut flowers contained enough carbohydrates to provide a total vase life of 14 days, which was estimated to be only 2 days less than that of intact flowers. In comparison, intact flowers contained an additional 3.2 g of sugars imported during flower opening, which amounted to nearly 42% of the total carbohydrates. For flowers that were stored 4 weeks, starch in the flower buds was almost completely hydrolyzed, producing similar hexose and higher sucrose concentrations than in fresh-cut stems. Store flowers opened more rapidly, 2 days versus the 5 days for fresh-cut stems, probably because the starch was already hydrolyzed, producing a shorter vase life

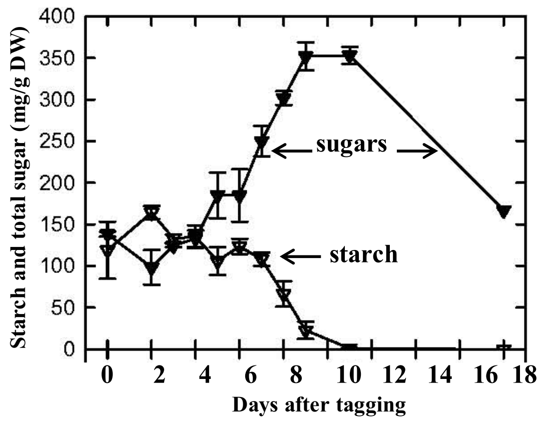

Fig. 8 Changes in the concentration of total sugars (full triangles) and starch (empty triangles) in peony bud/flower during opening and senescence. Bars = ±SE. Adapted from **Walton EF, McLaren GF, Boldingh L** (2007) Seasonal patterns of starch and sugar accumulation in herbaceous peony (*Paeonia lactiflora* Pall.). *Journal of Horticultural Science and Biotechnology* **82**, 365-370, ©2007, with kind permission from the Editor.

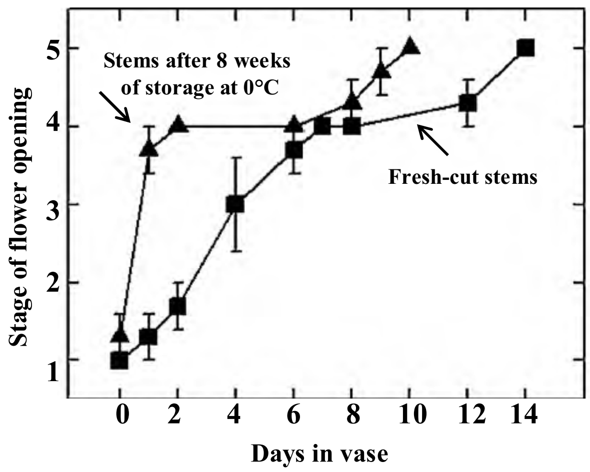

Fig. 9 Vase lives of fresh-cut peony stems (squares) and after 8 weeks of storage at 0°C (triangles). Stages of flower opening: 1 = tight bud, Stage 2 = loose bud, Stage 3 = almost open, Stage 4 = fully open, and Stage 5 = petals wilting. Bars = ±SE. Adapted from **Walton EF, McLaren GF, Boldingh L** (2007) Seasonal patterns of starch and sugar accumulation in herbaceous peony (*Paeonia lactiflora* Pall.). *Journal of Horticultural Science and Biotechnology* **82**, 365-370, ©2007, with kind permission from the Editor.

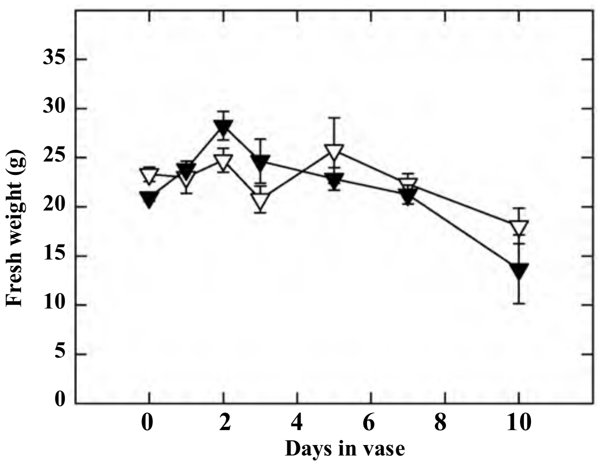

Fig. 10 Changes in fresh weights of non-stored fresh-cut (empty triangle) and stored peony buds/flowers (full triangle) during vase life studies. Error bars represent ±SEM. From **Walton EF, Boldingh HL, McLaren GF, Williams MH, Jackman R** (2010) The dynamics of starch and sugar utilisation in cut peony (*Paeonia lactiflora* Pall.) stems during storage and vase life. *Postharvest Biology and Technology* **58**, 142-146, ©2010, with kind permission from Elsevier, Amsterdam.

than fresh-cut stems. Single petaled flowers open more rapidly than those with multiple rows of petals (Walton *et al.* 2007). The authors (Walton *et al.* 2010) noted that flowers could be stored for 8 weeks and still have an "acceptable" vase life (**Figs. 9, 10**).

After dry storage, the stems should be recut and held in a hydrating solution (pH 3.5 using citric acid) at 21°C. A floral preservative should be used after the hydration of the flower stems (Heuser and Evensen 1986; Nowak and Rudnicki 1990). Sucrose pulsing can also be used to accelerate bud opening. Sang *et al.* (1998) tested 0, 5, 20 or 35% sucrose pulses for either 12 or 24 h and determined that 20% for 24 h provided the optimum solution uptake and fresh weight. Other chemicals have been tested including a 30 min pulse of uniconazol (20 mg L), which did not affect vase life (Hamada *et al.* 1989).

While peony buds are considered to have low sensitivity to ethylene (Dole and Wilkins 2005), Rogers (1995) recommended that ethylene levels during storage be as low as possible and that flowers not be exposed to exogenous ethylene. In addition, a 30 min pulse of 1 mM STS increased the vase life of cut herbaceous peonies by up to 2.5 days, depending on the cultivar (Hamada *et al.* 1989). Gast (2001) supported these results by noting that a 2-h pulse of 0.463 mM STS extended the vase life of 'Shawnee Chief' by up to 2.5 days.

Botrytis. Development of *Botrytis* is a major issue during postharvest handling and is one of the greatest limitations to storing cut peonies (Nowak and Rudnicki 1990). To reduce *Botrytis* problems, foliage should be dry (Armitage and Laushman 2003) and plastic sleeves should not be used (Dole and Wilkins 2005). Methyl jasmonate volatilized from a saturated pad enclosed in sealed bags with the stems reduced the disease incidence on buds stored for 6 weeks at 0°C, but not when stored for 8 or 10 weeks and did not affect vase life (Gast 2001).

Dried flowers. While the majority of cut peony flowers are used fresh, the flowers can also be air or freeze dried (Stevens *et al.* 1993; Gast 1995). Of course, the soft petals shrink considerably, but the medium to dark pink and red cultivars hold their color well. Light pink and white flowers tend to lose their attractive color and become pale brown (Rogers 1995). Double flowered types are generally used as they retain much petal mass after drying. One of the best varieties for drying is 'Sarah Bernhardt'. Flowers intended for drying can be disbudded, as for fresh sales, or the side buds can be left on the stem, increasing the amount of petal color on the final dried stem. Commercially cut flowers are air dried in dark rooms at 10°C or higher with 60% or lower humidity and ample air movement (Stevens *et al.* 1993). Foliage is removed from the stems, which are combined into bunches, often of 10 stems, and hung upside down. Flowers for drying are harvested when newly open. Harvesting later may cause the petals to fall before the stems are sufficiently dry.

PEONY GROWING AND PRODUCTION IN DIFFERENT REGIONS

Peony is highly appreciated worldwide as a beautiful garden plant, but, in addition, it is an ornamental crop with an increasing economic importance in global floriculture. In China, ornamental cultivars were developed in the 6^{th} to 7^{th} centuries from the medicinal plants of peony (Tsukamoto 1969). *P. lactiflora* was introduced to Japan before the 10^{th} century and subsequently many cultivars were created by selfing or crossing, especially during the middle Edo period (18^{th} century) to early Showa period (20^{th} century) (Tsukamoto 1984). Cultivars of *P. officinalis* were appreciated in European countries between the 15^{th} and 18^{th} centuries (Tsukamoto 1984; Wister and Holfe 1962). However, intensive breeding for flower shape and color began only in the 19^{th} century, when P. *lactiflora*, native to China, was introduced to Europe (Bailey 1916).

China

The peony is among the most popular flowers in ornamental culture in this country, which has one of the longest histories of cultivating ornamentals in the world (Wister and Holfe 1962; Li 1999; Uspenskaya 2002; Qi 2004). The peony, along with the plum blossom, is one of national emblems of China. It is also known as the "flower of riches and honor," and is used symbolically in Chinese art. During the T'ang dynasty (618-906) peonies became popular in the imperial gardens and were put under imperial protection. During the Sung dynasty, which began at the end of the 10th century, peony cultivation spread throughout China and the Sung capital of Louyang became a centre for peony culture. Louyang is still recognized today as a centre for peony culture, and dozens of peony exhibitions and shows are held there annually.

As new dynasties began and emperors moved their courts, peonies were also moved, further spreading the cultivation of peonies throughout China. During the Ch'ing dynasty of 1644 to 1911, the city of Caozhou became a centre of peony culture. Today this city is known as HeZe and is recognized as the second major peony centre of China. Like Louyang, HeZe holds an International Peony Fair in April each year. Both HeZe and Luoyang host a state funded research facility for peony research. More than 800 ha are dedicated to peony production in these regions. Commercial production is supported by much modern research on flowering physiology, manipulation (Yu *et al*. 2008; Cheng *et al.* 2009a, 2009b) and propagation (Zhang *et al.* 2006; Yu *et al.* 2008; Gao 2010) as previously described in this text.

Japan

Japanese breeders simplified the flowers and produced lighter, less complicated flower heads with rounded centers surrounded by smaller and wider petals, used to be called in Japanese *ebisugusuri* ("foreign medicine"), since its root was used as a treatment for convulsions. The Peony was also cultivated as a garden plant and was called the "prime minister of flowers" (Tsukamoto 1984). In 1948, Japanese breeder Toichi Itoh produced intersectional hybrids, which began the breeding of new intersectional varieties, known today as "Itoh Hybrids" (Smith 2004).

Japan is a major peony producer. Growers specialize in either tree or herbaceous peonies and are known for their grafting skills; therefore, a large percentage of the world's tree peony production originates from Japan.

Europe

Until the 18th century, European gardeners cultivated only the herbaceous species. Originally they were grown for their medicinal value, but later their ornamental qualities were appreciated. Tree peonies were brought to Europe in 1789 by Dr. Duncan and planted at Kew Gardens. Many tree peonies are still imported into Europe from Japan or China.

The popularity of peonies in Europe, and particularly in England, declined in the 20th century. Today, however, peonies are undergoing a renaissance of popularity throughout Europe, both as garden plants and as cut flowers. In addition to commercial production of cut flowers, peonies are very popular in European gardens, and several peony societies (German Peony Society, www.paeonia.de; Danish Peony Society www.danskpaeonselskab.dk; The (British) Peony Society www.thepeonysociety.org.uk) coordinate and share the experience of peony amateurs across Europe.

France. In the late 1800's to early 1900's, European plant breeders J. Calot, F. Crousse, A. Dessert, V. Lemoine, N. Lemon, and E. Méchin worked mainly with *P. lactiflora* to produce numerous varieties, such as 'Le Printemps' and 'Avant Garde', which are still popular. Currently, peony production is concentrated in southeast France, where cultivated areas have increased 10 fold in the last 15 years (Jacob *et al.* 2006). Contemporary breeding is conducted mainly by many specialized amateur peony aficionados. Only a small number of professionals or companies seem to be involved in breeding peonies (Jacob *et al.* 2006). In 2008, the annual supply of peony cut flowers from France to the international market reached 1.1 million stems (Looze *et al.* 2008).

The Netherlands. This small country produces the most peonies worldwide. Dutch producers sell more than 48 million stems annually (Looze *et al.* 2008) and are the main producers of plant material for foreign peony growers. A large number of cultivars are grown, approximately 50 varieties, with five of them, 'Sarah Bernhardt', 'Karl Rosenfeld', 'Dr. Alexander Fleming', 'Duchesse de Nemours' and 'Shirley Temple', being the most popular.

England. Kelway and Son nursery introduced into England nearly 300 peonies in the 19th century. In the 1930's Kelways was reputed to have made a perfume, "Peony Valley", from peony petals. Today Kelways is the UK's oldest and largest grower and supplier of quality herbaceous and tree peonies (www.kelways.co.uk). Although peonies have been in and out of fashion since medieval times, recent Chelsea Flower Shows have revived interest in this flower, because many of the Gold Medal winning gardens included an abundance of herbaceous peonies.

North America

Although two peony species are native to the western United States, the first species grown in gardens was apparently *P. officinalis* (Fearnley-Whittingstall 1999). While the first printed references to peonies were not known until 1806, the plant is thought to have been cultivated in North America earlier. At the time, five types of peonies were listed, one of which was *P. albiflora*, the white-flowered peony, which later became known as *P. lactiflora*. Subsequently, the peony was listed in many horticultural references and catalogues. In the mid 1800s, the introduction of numerous *P. lactiflora* cultivars led to its becoming the dominant type in the USA. Harding (1917) documented that 30 varieties were cultivated in 1858, of which at least two are still available today: 'Festiva Maxima' and 'Edulis Superba'. Several breeders, including H.A. Terry, J. Richardson, G. Hollis, and T.C. Thurlow from Iowa and Massachusetts, became interested in peonies in the mid to late 1800s and a multitude of garden cultivars appeared over the next few decades. By 1904, interest in peonies was so great that the American Peony Society (APS) was first organized. One of the first major undertakings of the fledgling APS was a project with Cornell University to study the commercial value of peonies and to clarify their nomenclature. Over a period of several years, members of the APS and horticulturists at Cornell University studied the collection and compiled a list of about 500 distinct varieties.

One of the most well-known peony breeders in North America was Arthur P. Saunders. Born in Canada, he became a chemistry professor at Hamilton College in Clinton, New York. He developed some of the most beautiful varieties, still known today. Other breeders providing important contributions include John, Charles, and Carl Klehm, L. Glasscock, W. Krekler, E. Auten, M. Bigger, W. Bockstoce, A. Brand, the Wilds, R. Tischler, D. Reath, W. Gratwick. Although fewer people are now breeding peonies, D. Hollingsworth and R. Anderson are still actively working with them.

Commercially, cut peonies have a long history in North America. Wholesale production dates back to at least 1884 when Amasa Kennicott sold cut flowers for $0.01 U.S./stem to Chicago florists (Rogers 1995). By the early 1900s, the peony was a highly valued cut flower in the United States, used primarily for the Memorial Day holiday (late May). By the 1920s hundreds of thousands of stems were being shipped, often by refrigerated railway cars, to many cities. At one time, more than 1620 ha were in production in the

Midwest, primarily in Indiana and Illinois (Post 1949). Interest in and production of peonies has fluctuated over the years, especially declining during the 1970s and 1980s. Today, the peony has returned as a specialty cut flower with production from North Carolina on the East Coast to Kansas in the Midwest, and to Oregon and northern California on the West Coast. While much of the peony production is sold locally by small producers, large wholesale growers can be found in Arkansas, Illinois, North Carolina, Oregon, and Wisconsin. A fledgling but rapidly growing cut peony industry has developed in Alaska, taking advantage of its far northern location to allow natural flowering of peonies in June, July and August (Auer and Holloway 2008). The APS is still flourishing today with members from around the world. It holds the official repository for peony registrations, annual exhibitions and shows and publishes an informative quarterly bulletin.

As with the United States, peonies are a beloved garden perennial and cut flower in Canada. Due to their excellent cold hardiness peonies are grown throughout Canada, except for the very far north. Commercial production of crowns and cut flowers takes place in many locations, especially in Ontario and British Colombia. Large scale cut flower production occurs mainly in British Columbia, some of which is marketed through the Vancouver Flower Auction.

The Canadian Peony Society (CPS) was created in 1998. It produces a quarterly bulletin dedicated to sharing the experiences of Canadian peony enthusiasts, to encourage peony breeding, to produce distinctly Canadian peony hybrids and to coordinating an annual National Peony Show.

Russia

Botanical studies of peonies in Russia can be attributed to 1733, when Peter Simon Pallas described more than 10 wild species. Numerous species were identified in Russia and neighboring areas and today the local flora is documented to contain more than 20 species (Cherepanov 1995). The first garden varieties of peonies were introduced to Russia in the 17th century, during the monarchy of Peter the Great. They were cultivated in so-called apothecary gardens for medical and botanical studies. At the beginning of the 19th century, several varieties from French breeders were imported from Europe and were grown in the botanical gardens and private collections of Russian aristocrats (Rubinina 2009).

After World War II, garden peonies became widely cultivated. Many government and scientific institutes gathered significant collections of peonies. Numerous professionals and flower amateurs have taken part in the selection and breeding of local varieties in Moscow, St. Petersburg, Riga, Kiev and other regions. Recent publications (Dudik and Harchenko 1987; Kapinos and Dubrov 1993; Uspenskaya 2002; Rubinina 2009) provide up-to-date information on local and introduced varieties and cultivation methods of garden peonies in Russia. Data on commercial production of cut flowers is not available.

Israel

Peony cultivars were introduced to Israel in the early 1990s. It was quickly apparent that growing peonies in a warm Mediterranean climate was quite challenging and required precise knowledge of plant development. Research on flowering physiology and adaptation to local environmental conditions has provided a basis for the practical production and forcing systems of peony cut flowers for the early market niches (Halevy *et al.* 2002; Kamenetsky *et al.* 2003; Halevy *et al.* 2005), and for developing several practical methods for cut flower production (**Fig. 11**):

1. Plant Reposition: plants are grown in containers and provided with all the necessary environmental conditions for optimal flower development. This method requires precise control of plant development and an in-depth knowledge of the flower's initiation process. With this method a very early crop can be obtained from mid-January onward.
2. Plastic Tunnels: field-grown plants in uncovered greenhouses are exposed to ambient cold temperatures until they receive a sufficient number of predetermined chilling units. Plants are then covered with plastic sheets to increase temperatures. This method requires precise temperature control during dormancy breaking and stem elongation. The resulting plants flower about one month earlier (March-April) than plants grown in open fields.
3. Open Plot: plants are grown in open plots and in net-covered houses for cut flower production in April-May.

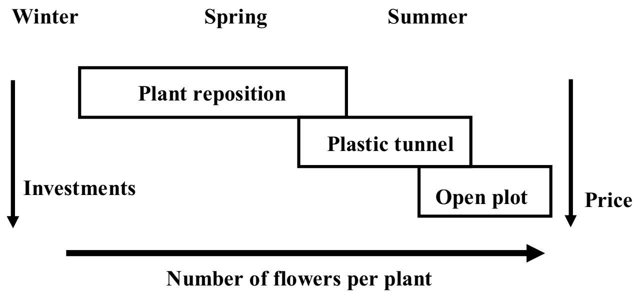

Fig. 11 Strategies for commercial production of herbaceous peonies in Israel. Note differences in investment to production, price in international market, and production of flower stems per plant with each strategy. Adapted from **Kamenetsky R, Barzilay A, Cohen M** (2007) Herbaceous peony for cut flower production: Flowering physiology and cultivation techniques. *Acta Horticulturae* **755**, 121-126, ©2007, with kind permission from the ISHS, Leuven, Belgium.

The advance of new technologies for peony cultivation, in combination with an in-depth knowledge of plant physiology and requirements, has allowed the speedy and effective development of a new and promising branch of ornamental horticulture in Israel. In 2010, high quality cut flowers of the two most popular varieties 'Sarah Bernhardt' and 'Duchesse De Nemours' were produced on *ca.* 50 ha. Twenty other varieties, popular in Europe and the USA, have recently been introduced to Israel and are being evaluated under local conditions.

Southern Hemisphere

In general, field production of peonies for cut flowers has a relatively short harvest season. In most areas of Europe, the USA and Canada peonies can be harvested from mid-April in warmer regions to June in the cooler latitudes. At any one location, a wide variety of cultivars are grown and the harvest season is approximately 6 weeks, if the weather is cool and shorter if warm. However, demand for peonies in the global market has become year-round. With the advent of rapid, relatively inexpensive air freight, Chile and New Zealand in the Southern Hemisphere have seized the opportunity to provide cut peonies during their spring and early summer, from late October (northern Chile, New Zealand) through January (southern Patagonia). Other countries are also producing small amounts of cut peonies including Australia and South Africa.

In Chile, cut peony exports have increased from $158,000 US in 2002/03 to $802,700 in 2008/09, most of which was sent to the United States and much smaller amounts to the Netherlands, United Kingdom, Japan, and Germany (Fundación para la Innovación Agraria 2008; Sáez Molina 2012). Peonies are grown from south of Santiago in central Chile to Region XII, the southernmost region in Chile. In the main production areas, harvest begins in mid November in Region IX, which is in south central Chile around Temuco, and ends in mid to late January in Region XII.

The peony has become important enough in New Zealand that several research projects have been conducted in the country (Fulton *et al.* 2001; Hall *et al.* 2007; Walton *et al.* 2007, 2010). In New Zealand, the majority of cut stems

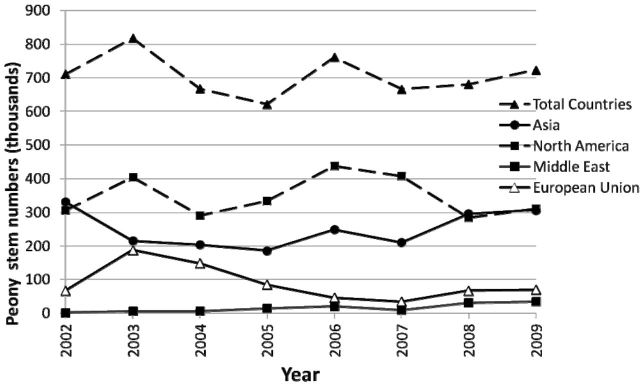

Fig. 12 Cut peony stem exports from New Zealand. Source: Statistics New Zealand, provided by Keith Funnell.

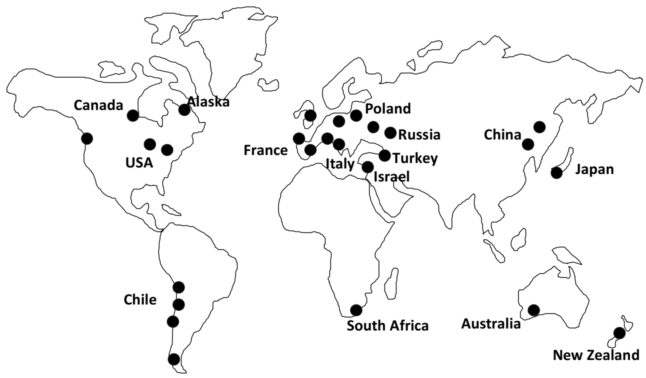

Fig. 13 Schematic presentation of global production of peony cut flowers in different countries and regions.

are grown on the South Island, primarily in Nelson, Canterbury, Otago and Southland (K. Funnell, pers. comm.). Some production also occurs on the North Island. Approximately 600,000 to over 800,000 stems were exported each year from 2001 to 2009, with North American being the leading importer (**Fig. 12**; K. Funnell, pers. comm.).

COMMERCIAL PRODUCTION OF CUT FLOWERS

Cut peonies are grown around the world for both local and international markets (**Fig. 13**). The main production of peony flowers in the Northern Hemisphere occurs in May-June, with limited production in June-August in Alaska. Israel, Italy and France produce cut flowers in January-April, while in the Southern Hemisphere (Chile, New Zealand, Australia) the main production occurs in October-December.

The Netherlands produces the most cut peonies, with approximately 55 million stems annually. In addition, *ca.* 5 million cut stems are imported annually into the Dutch auction facilities. At the Dutch floral auctions, the number of stems sold has increased from 13 million stems in 1998 to 50 million in 2007. In 2011 the number of stems sold reached 67 million, while only in January-July 2012 62 million stems were sold (FloraHolland 2012). The turnover in the Dutch auctions increased from in 2007 €20.5 to 27.9 million, and the peony was ranked number 18 out of 153 taxa. In a few years, the number of stems sold is expected to reach 100 million, while more flowers are sold outside of the traditional early summer production period.

Other major cut stems producers include Israel, France, Germany, Hungary, Poland, and the United States, although for the latter most of the production is sold domestically . A number of other countries have begun to produce cut flowers commercially, including Australia, Chile, China, Italy, Kenya, New Zealand, Portugal, South Africa, Tunisia, and Turkey.

Among the several thousands available cultivars, only a small number are able to produce high quality fresh-cut flowers (Gast *et al.* 2001; Cheng *et al.* 2009a; Li *et al.* 2009). Despite on-going breeding efforts in China, France, the United States, and other countries, the most important varieties have been on the market for many years (**Table 3**). The top ranked cultivar in the Netherlands and the United States is 'Sarah Bernhardt', due to its productivity, color and reliability.

CONCLUDING REMARKS

Peony is one of the most popular garden plants in temperate regions. Thousands of years ago, it was introduced into cultivation in China, and has since spread widely to many countries. Numerous varieties have been developed to satisfy the demand for new colors, fragrance, earliness or lateness, and disease resistance. In the last two decades, peonies have, once again, become popular as cut flowers. This development has created new demands for biological research and the development of production and postharvest technologies. Today, more than 25 countries produce cut peony flowers, with the primary markets in Europe, the USA, and Canada. Cut peony flowers are highly valued in international markets, but are only available for a short time in late spring and early summer in any given production location.

Despite the popularity of cut peonies, several reasons restrict its production and use: long juvenile period, lack of efficient systems for mass propagation and long-term postharvest storage, complicated flowering physiology, and botrytis during postharvest handling. Recent research has significantly promoted the production of high-quality cut flowers.

In general, peonies are grown successfully in temperate, cold-winter climatic zones. Recent development of peony cultivation in Israel, Italy and southeast France aims to fulfill a high demand for early market niches, while cultivation in the Southern Hemisphere provides peony supply during the late seasons in October-January. A recently project in Alaska will bridge the cut stem production between North Europe and USA with production in the Southern Hemisphere. Finally, the global peony network can provide a year-round supply of high-quality cut flowers to international and local markets.

Over recent decades, we have learned that, for successful commercial production breeding of new varieties, in-depth studies of plant development and the improvement of production and shipping techniques are essential. New

Table 3 Top-ten varieties of herbaceous peonies, sold in United Flower auctions (The Netherlands) in 2008 (adapted from Looze *et al.* 2008)

Ranking	Variety	Colour	Stems sold in United Flower Auctions (2008)
1	Sarah Bernhardt	pink	20,471,026
2	Karl Rosenfeld	bright crimson	5,133,646
3	Dr. Alexander Flemming	salmon pink	3,387,955
4	Duchesse De Nemours	cream white	3,271,806
5	Shirley Temple	white	2,557,066
6	Flame	pink	2,442,962
7	Kansas	pink	1,210,112
8	Krinkled White	white	819,202
9	Monsieur Jules Elie	purple	590,480
10	Edulis Superba	pink	508,745

products and techniques must be developed by researchers and breeders in collaboration with efficient producers and satisfied consumers. All components of the production and marketing chain must be linked together in mutually beneficial ways. In the future, special attention should be also given to the identification of diseases and viral infections, their control and environmentally-friendly methods of prevention.

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