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Edited by
IAN WARRINGTON

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HORTICULTURAL REVIEWS

Volume 45

Edited by
Ian Warrington

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Contents

| | |
|--|-------------|
| Contributors | ix |
| Dedication: Jules Janick <i>Ian Warrington</i> | xiii |
| 1. The Flowers of <i>Fragaria × ananassa</i>: Morphology, Response to Photoperiod, and Genetics of Induction <i>Andrew Petran and Emily Hoover</i> | 1 |
| I. Introduction | 2 |
| II. Strawberry Growth, Reproduction, and Commercial Management | 2 |
| III. Inflorescence Architecture | 13 |
| IV. Genetics of Flower Induction | 16 |
| V. Conclusions | 26 |
| Literature Cited | 27 |
| 2. Small Unmanned Aircraft Systems (sUAS): An Emerging Technology for Horticulture <i>James A. Robbins</i> | 33 |
| I. Introduction | 35 |
| II. Aircraft | 36 |
| III. Sensors and Data Processing | 42 |
| IV. Horticultural Applications | 52 |
| V. Challenges | 61 |
| VI. Conclusions | 64 |
| Literature Cited | 64 |

| | |
|---|------------|
| 3. Leaf Blackening: A Serious Impediment to Long-Term Cold Storage, Transport, and Extended Vase Life in <i>Protea</i> Cut Flowers | 73 |
| <i>Eleanor W. Hoffman, Waafeka Vardien, Gerard Jacobs, and Nicole E. Windell</i> | |
| I. Introduction | 74 |
| II. Variation in Expression of Leaf Blackening | 76 |
| III. Physiological Causes of Leaf Blackening | 80 |
| IV. The Biochemical Mechanisms of Leaf Blackening | 87 |
| V. Control of Leaf Blackening | 90 |
| VI. Conclusions | 99 |
| Literature Cited | 100 |
| | |
| 4. Sapota (<i>Manilkara achras</i> Forb.): Factors Influencing Fresh and Processed Fruit Quality | 105 |
| <i>Babak Madani, Amin Mirshekari, Elhadi Yahia, and John B. Golding</i> | |
| I. Introduction | 107 |
| II. Nutritive Value | 111 |
| III. Physiological and Biochemical Changes During Fruit Maturation and Ripening | 114 |
| IV. Preharvest Effects on Postharvest Quality | 120 |
| V. Physiological Disorders | 121 |
| VI. Postharvest Diseases | 122 |
| VII. Postharvest Technology | 123 |
| VIII. Postharvest Treatments | 126 |
| IX. Non-Destructive Methods for Identifying Fruit Maturity and Quality | 131 |
| X. Processing | 132 |
| XI. Summary and Future Prospects | 134 |
| Literature Cited | 136 |
| | |
| 5. The Citron (<i>Citrus medica</i> L.) in China | 143 |
| <i>David Karp and Xulan Hu</i> | |
| I. Introduction | 145 |
| II. History and Culture | 145 |
| III. Nomenclature | 147 |
| IV. Current Citron Cultivation in China | 148 |

| | |
|--|------------|
| V. Major Cultivars of Chinese Citron and Select Citron Hybrids | 158 |
| VI. Germplasm Status; Regional and Global Perspective | 190 |
| Literature Cited | 192 |
| 6. Apple Rootstocks: History, Physiology, Management, and Breeding | 197 |
| <i>Richard P. Marini and Gennaro Fazio</i> | |
| I. Introduction | 198 |
| II. History | 199 |
| III. Rootstock–Scion Interactions | 204 |
| IV. Stresses Influencing Rootstock Performance | 225 |
| V. Interstems | 259 |
| VI. Influence of Rootstock on Fruit Characteristics | 262 |
| VII. Genetics and Breeding | 266 |
| VIII. Rootstock Evaluation | 277 |
| Literature Cited | 282 |
| 7. Canopy Growth and Development Processes in Apples and Grapevines: Responses to Temperature | 313 |
| <i>Dennis H. Greer</i> | |
| I. Introduction | 315 |
| II. Phenology | 316 |
| III. Dormant Buds in Apple Trees and Grapevines | 317 |
| IV. Winter Chilling in Apple Trees and Grapevines | 319 |
| V. Budbreak and Shoot Development in Apple Trees and Grapevines | 320 |
| VI. Fruit Growth | 332 |
| VII. Biomass Partitioning | 338 |
| VIII. Photosynthesis and the Carbon Economy | 340 |
| IX. Abiotic Stress Effects on Canopy Physiology | 349 |
| X. Impact of Climate Change on Phenology | 355 |
| XI. Conclusions | 357 |
| Literature Cited | 358 |
| 8. Organic Acids in Fruits: Metabolism, Functions and Contents | 371 |
| <i>Robert P. Walker and Franco Famiani</i> | |
| I. Introduction | 373 |
| II. The Function of the Flesh of Fruits and its Implication for their Organic Acid Contents | 375 |

| | |
|--|------------|
| III. Acids that Contain a Benzene Ring: The Aromatic Acids | 377 |
| IV. The Inter-Related Acids: Ascorbic, Oxalic, Tartaric, and Galacturonic | 385 |
| V. Fatty Acids | 398 |
| VI. Malic, Citric, and Metabolically Related Acids | 399 |
| VII. Conclusions | 412 |
| Literature Cited | 413 |
| Subject Index | 431 |
| Cumulative Subject Index | 435 |
| Cumulative Contributor Index | 473 |

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Jules Janick

Dedication: Jules Janick

Dr Jules Janick, James Troop Distinguished Professor of Horticulture in the Department of Horticulture & Landscape Architecture at Purdue University, is undoubtedly one of the most well known and well regarded horticultural scientists in the world today. As the founder of *Horticultural Reviews*, and the related *Plant Breeding Reviews*, he is highly deserving of having this volume dedicated to him. His contributions to horticultural science have been extensive, embracing many aspects of the discipline. He has been truly international in his endeavors.

Jules was born in New York City in 1931, and graduated with a B.S. in Agriculture from Cornell University in 1951. This was followed by an M.S. (1952) and a Ph.D. (1954) – both at Purdue University in genetics and breeding. He was 23 years old at the completion of the Ph.D. – an early indication of his commitment and productivity!

Within his career in horticultural research, Jules and his students (13 masters and 17 doctoral) have made important advances in the genetics of sex determination, including the synthesis of heteromorphic sex chromosomes in spinach, fire blight resistance, cleistogamy, cucurbitacins, artemisinin production, anthocyanin pigmentation, plant density, *in vitro* metabolite production from somatic embryos, and the production of synthetic seed. In crop improvements he has been associated with the release of 21 scab-resistant apple cultivars, three pear cultivars with tolerance to fire blight, delayed-bolting arugula, crack-resistant tomato (for Brazil), and the first release of a cultivar (pelargonium) from somaclonal variation.

In a particular niche area of study, Professor Janick has made contributions to the historical aspects of horticulture, with emphasis on ancient Egypt and the New World, and has explored the relation of art and horticultural technology with special studies on the iconography of *Rubus*, *Daucus*, the Cucurbitaceae, the Solanaceae, and opening up a new approach to the study of plant diversity, origins, cultivar evolution, and diversity. He has contributed iconographic studies on Dioscorides, the Drake Manuscript, the Unicorn Tapestries, Caravaggio, Cotan, and

the Raphael frescoes in the Villa Farnesina in Rome. He has written on the inter-relationship of horticulture and scholarship, art, ethics, and the contributions of horticulture to human welfare. At present, he is immersed with Dr Arthur Tucker in the unraveling of the bizarre Voynich Codex, demonstrated to be a 16th century Mesoamerican herbal.

Professor Janick has taught many courses, including genetics, horticultural plant breeding, seed production, plant propagation, tropical horticulture, and the history of horticulture. The last two courses are now offered continuously online with over 500 students per year.

Jules has been a prolific author and editor in horticultural science. He was the editor of *HortScience* from 1970 to 1983 (14 volumes) and transformed it into one of the major journals in horticulture. He was editor of the *Journal of American Society for Horticultural Science* (ASHS) from 1976 to 1983 (8 volumes). He is the founder and editor of both *Horticultural Reviews* (44 volumes since 1979) and *Plant Breeding Reviews* (40 volumes since 1983), one of his major achievements. From 2002 to 2010 he was the science editor of *Chronica Horticulturae* (International Society for Horticultural Science, ISHS), and transformed this publication into a significant magazine of world horticulture. He has edited and produced seven proceedings of New Crops symposia since 1990 that have had a deep impact on new crop information. The development of a new crop website (www.hort.purdue.edu/newcrop) has become a major world resource for information on crops.

Professor Janick is the author of the book *Horticultural Science* (4 editions), an influential text that has been translated into Spanish, Portuguese, Arabic, and Hindi. Another text – *Crop Science; An Introduction to World Crops* – has gone through three editions. He has organized a number of monographs on fruit breeding, including *Advances in Fruit Breeding* (translated into Chinese, Russian, and Spanish), *Methods in Fruit Breeding*, and a three-volume update of *Advances* entitled *Fruit Breeding*. Jules has edited eight volumes of *Acta Horticulturae*. Altogether, he has authored, co-authored or edited over 140 volumes of books, journal volumes, proceedings, and monographs. Dr Janick also co-edited the CABI *Encyclopedia of Fruit and Nuts* (2008). He has authored 61 book chapters and 427 papers, of which half are in refereed journals.

Jules had the vision to initiate *Horticultural Reviews* in 1979. At that time, reviews on horticultural topics were limited in both length and scope, and did not do justice to the volume of horticultural research that had been conducted particularly in the latter half of the 20th century. This new publication fulfilled that niche and has grown to be a valued source of information for scholars, scientists, and horticulturists worldwide.

A total of 349 review articles, comprising 18 936 pages in aggregate, have been included in the 44 volumes published to date (noting that in some years more than one volume was published). Each volume is dedicated to a horticulturist. Throughout that period Jules remained the sole editor, soliciting manuscripts, cajoling authors to deliver by the due date, and editing the copy received. He was tireless in each of these pursuits. In 1983 he founded *Plant Breeding Reviews* (40 volumes), with about half the articles devoted to horticultural crops.

The impact that Jules Janick has had on horticulture has not been confined to the USA. He served two years at the Rural University of Minas Gerais in Brazil in 1963–1965 as part of a USAID Purdue contract, where he lectured in Portuguese. The list of countries that he has visited while participating in meetings, consulting, conducting research, advising, and teaching is extensive, and includes Argentina, Australia, Bahamas, Belgium, Canada, Canary Islands, Columbia, Costa Rica, Crete, Ecuador, Egypt, England, Finland, France, Germany, Hungary, Indonesia, Israel, Italy, Ivory Coast, Japan, Korea, Mexico, Morocco, New Zealand, Norway, People's Republic of China, Poland, Portugal, Puerto Rico, Spain, Sweden, The Netherlands, Tanzania, and Turkey.

Among his numerous recognitions are several awards of ASHS, the Wilder award of the American Pomological Society, corresponding member of the Italian Academy of Agriculture, and four honorary degrees [University of Bologna (1990), the Technical University of Lisbon (1994), the Hebrew University of Jerusalem (2007), and University of Agricultural Sciences and Veterinary Medicine, Cluj-Napoka, Romania]. He served as President of the American Society for Horticultural Science in 1986–87, and was inducted to the ASHS Hall of Fame in 2009. In 2011 he received the Lifetime award of the National Association of Plant Breeders. He also served on the Board of the ISHS for two terms (2002–2010). He is a Fellow of the ASHS (1976), of the Portuguese Horticultural Association (1981), the ISHS (2006), and is an ISHS Honorary Member (2010).

In the nomination of Professor Janick for the ASHS Hall of Fame Award in 2008, Dr Fred Bliss (Professor Emeritus at the University of California, Davis) stated the following:

“Seldom, if ever, has anyone made the breadth and depth of contributions to the field of horticulture as Jules has done. Whether a person is a professional horticulturist or hobbyist, in academia or business, breeder or physiologist, author or reader, you likely would have heard about and benefited from Jules' multiple interests. In addition to his numerous contributions to teaching and extended education in the academic setting, he is a teacher in the broadest sense by virtue of his tireless efforts

to expound and promote horticulture by research, scientific publications, and wonderful oral/visual presentations.”

In the same nomination, Dr Martin J. Bukovac (Professor Emeritus at Michigan State University) stated:

“He is an individual with a missionary commitment to advance horticulture locally, nationally and internationally through his extensive lecturing, writing, advising and organiser of conferences. He has rekindled an interest in the art and history of horticulture – and is probably the world’s authority in both.Jules is a human catalyst in bringing people together from various disciplines, nationally and internationally, in organising projects, publications, and conferences and seeing them to fruition. One look at his CV confirms that Jules is an outstanding educator, scientist and horticulturist....”.

Jules, the Renaissance man, is the poet laureate of the Horticulture Department and a talented artist. Throughout his career, Jules has been ably supported by Shirley, his wife of 64 years. They have a son, Peter, a daughter Robin, and four grandsons, Noah, Lee, Nathan, and Aaron. He regards his family as his greatest achievement. His credo has been that advances in horticulture throughout the centuries represent some of the greatest human accomplishments for the betterment of humanity and he is strongly committed to the view that horticulture provides food for body and soul.

IAN WARRINGTON
Emeritus Professor
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New Zealand

In 2016, Jules passed the editorship of *Horticultural Reviews* to Dr Ian Warrington, and of *Plant Breeding Reviews* to Dr Irwin Goldman, who have undertaken to keep retain the high standards that have been set for these two important publications.

The Flowers of *Fragaria* × *ananassa*: Morphology, Response to Photoperiod, and Genetics of Induction

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ABSTRACT

The common cultivated strawberry (*Fragaria* × *ananassa*) is a healthy and popular fruit throughout the world, but its octoploid genetic structure poses difficulties to breeders, and the plant's flowering response to temperature and photoperiod has been challenging to predict, resulting in multiple flowering phenotypes throughout the commercial germplasm. This review assesses the morphology and physiology of these phenotypes, the cultural practices which are common to each flowering response, and focuses on recent efforts to map the genetic basis of day-neutrality within *F.* × *ananassa* and its progenitor *Fragaria vesca*. We summarize the recent consensus observing that the genetics of day-neutral flower induction in diploid *F. vesca* and octoploid *F.* × *ananassa* are not orthologous, and discuss the variance of findings regarding determination of day-neutrality in octoploid cultivars.

KEYWORDS: strawberry, day-neutral, diploid, octoploid

I. INTRODUCTION

II. STRAWBERRY GROWTH, REPRODUCTION, AND COMMERCIAL MANAGEMENT

A. Vegetative Growth

B. Flower Structure

C. Flower Induction, Initiation, and Development

1. June-bearing

2. Everbearing and Day-neutral
 3. Thermophotoperiod and Temperature Effects
- III. INFLORESCENCE ARCHITECTURE
- IV. GENETICS OF FLOWER INDUCTION
- A. *Fragaria vesca*
 - B. *Fragaria* × *ananassa*
- V. CONCLUSIONS
- LITERATURE CITED

I. INTRODUCTION

The strawberry (*Fragaria* spp.) is one of the most widely distributed fruit crops in the world. Production of the fruit is present in almost every continent and has exceeded 4 million tonnes per year since 2007 (Wu *et al.* 2012). There is considerable genetic diversity within strawberry germplasm; wild diploid through decaploid plants have been discovered (Stewart and Folta 2010). This diversity leads to genotypic and phenotypic variance even within the same strawberry species. Perhaps the most commercially important variance is that of flowering habit within the commercially cultivated strawberry *Fragaria* × *ananassa*.

Because of its commercial value and popularity, the strawberry is a thoroughly documented fruit crop. The purpose of this review is to compile and contrast the morphologic and physiologic traits of *F.* × *ananassa* flowering types and review the most recent efforts to identify the underlying genetics behind flowering habit.

II. STRAWBERRY GROWTH, REPRODUCTION, AND COMMERCIAL MANAGEMENT

A. Vegetative Growth

The strawberry plant is an herbaceous perennial with short internodes forming a modified stem rosette (Savini *et al.* 2005). This modified stem is commonly known as a crown, where long-petiole trifoliate leaves and axillary meristems converge spirally around its axis, ending in a terminal inflorescence (White 1927). Strawberry leaves present a typical dicotyledonous structure with long petioles and foliaceous basal stipules (Savini *et al.* 2005). Leaf lifespan can exceed three months in favorable conditions (Poling 2012). Axillary meristems can differentiate into branch crowns, which stay near and are structurally identical to the original crown, or *stolons* (also called *runners*), which give rise to separate daughter plants (Fig. 1.1) (Demchak 2010). Crowns typically

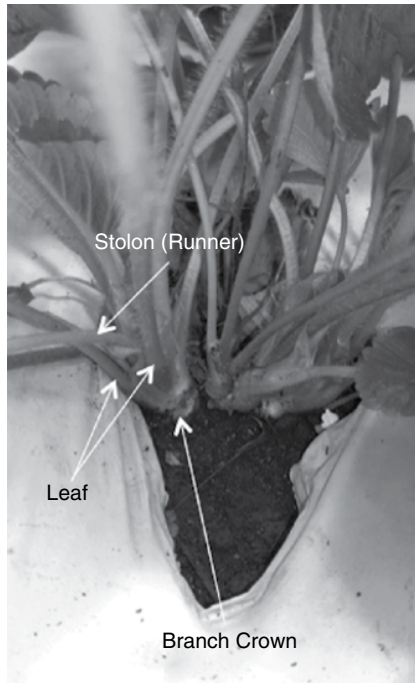


Fig. 1.1. Leaves and axillary meristems of cultivar ‘Portola.’ Photograph taken August 9, 2016, in Minnesota.

produce one to two branch crowns in a season, but have been known to produce more than five; from a production standpoint, three to four total crowns per plant is desirable, as more can result in decreased fruit size (Poling 2012).

B. Flower Structure

Inflorescences have two internodes, and develop terminally on the crown or branch crown of the plant in a structure known as a *dichasial cyme* (Savini *et al.* 2005). Dichasial cymes have a terminal, primary flower branch with opposite secondary branches beneath the terminal bud, leading to secondary flowers. In strawberry, the inflorescence is commonly known as a *flower cluster*, and the primary flower, known as the “king flower,” typically bears the largest fruit. Secondary branches begin at the juncture of the first and second internodes; some inflorescences also have tertiary and quaternary branches and flowers (Fig. 1.2).

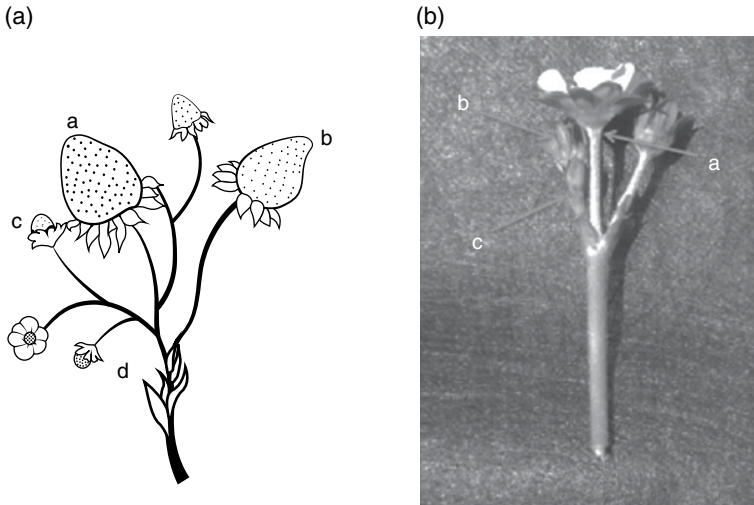


Fig. 1.2. (a) Diagram of fully developed flower cluster with (a) primary flower, (b) secondary flower, (c) tertiary flower, and (d) quaternary flower <http://www.hort.cornell.edu/grower/nybga/pdfs/2012berryproceedings.pdf> (from Poling 2012). (b) Picture of a flower cluster of the cultivar 'Portola', with (a) primary flower, (b) secondary flower bud, and (c) tertiary flower bud. Photograph taken July 10, 2014, in Minnesota.

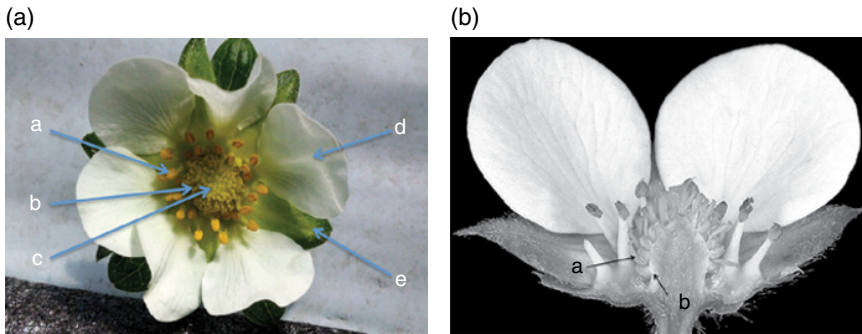


Fig. 1.3. (a) Principal flower parts of cultivar 'Evie-II,' including (a) stamen, (b) pistil, (c) receptacle, (d) petal, and (e) sepal. Photograph taken July 10, 2014 in Minnesota. (b) Cross-section of *F. × ananassa* showing (a) pistil and (b) receptacle. Photograph obtained, with permission, from G.D. Carr, December 9, 2015; http://www.botany.hawaii.edu/faculty/carr/images/fra_sp.jpg.

The principal parts of the flower itself are shown in Fig. 1.3. Strawberry flowers have five sepals; fleshy green structures beneath the petals which enclose the flower at bud stage and eventually become the “calyx,” or cap of the berry. Stamens discharge pollen and fertilize the pistils, which are secured on a conical stem known as the receptacle.

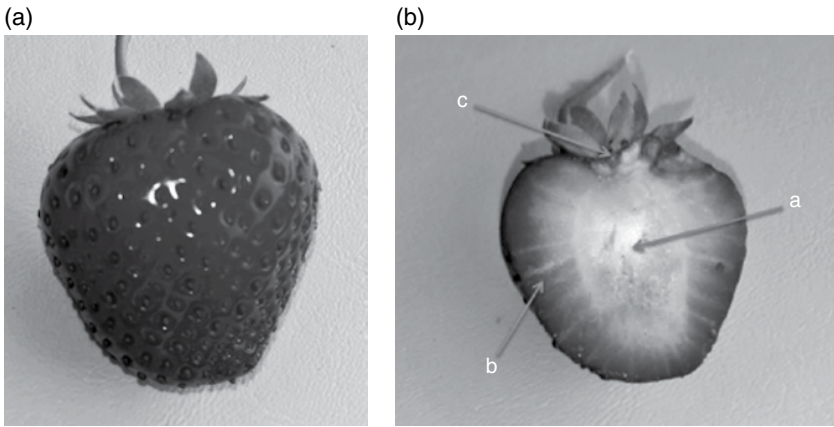


Fig. 1.4. (a) Profile of mature fruit of the cultivar ‘Amandine,’ with embedded achenes. (b) Cross-section of an ‘Amandine’ fruit, with (a) interior receptacle, (b) fibrovascular tube and (c) calyx. Photograph taken July 10, 2014, in Minnesota.

This receptacle becomes the full, fleshy “berry” at fruit maturity. Despite this plant’s common name, the fruit itself is not botanically classified as a berry. The seed-like organs embedded on the epidermis of the receptacle are actually modified dry fruits known as *achenes*. The achenes are each connected to the interior of the receptacle by fibrovascular strands, and hold the true seed within their pericarp (Fait *et al.* 2008) (Fig. 1.4). In *F. vesca*, auxin and gibberellin biosynthesis occurs in the endosperm and seed coat of the developing achenes, which in turn triggers maturity of the surrounding receptacle (Kang *et al.* 2013). Because the strawberry fruit contains multiple achenes, and is comprised of a receptacle in addition to its ovaries, it can be classified both as an aggregate and as an accessory fruit.

C. Flower Induction, Initiation, and Development

Flower induction, initiation and development are highly variable by cultivar, and dependent on genotypic responses to temperature and photoperiod (Savini *et al.* 2005; Stewart and Folta 2010). These responses are commonly grouped into three flowering categories: June-bearing; everbearing; and day-neutral. Strawberry cultivars are typically classified under one of these three categories based on their photoperiodic flowering habits, and it was originally assumed these habits remained constant over a wide range of temperatures (Darrow and Waldo 1933). However, further research led to the discovery that the photoperiod response of many cultivars would be altered if

temperatures were either sub- or supraoptimal (Guttridge 1985; Nishiyama and Kanahama 2000; Sonstebly and Heide 2007). This interaction of temperature with photoperiod, known as *thermo-photoperiod*, adds a quantitative factor to the original categorical classifications. Indeed, some believe it incorrect to assign broad flower habit categories to strawberry at all, as photoperiod responses appear to be cultivar-specific (Durner 2015). However, as the vast majority of strawberry-based publications use these classifications, this review will utilize them as well, with the implicit understanding of variance and interaction even within each flowering type. In this section, photoperiod response and common cultural practices of the three groups assuming optimal temperature conditions will first be discussed. The way in which the responses have been observed to change under different temperature ranges will then be explored.

1. June-bearing. Natural flowering patterns of cultivated octoploid strawberry, *F. × ananassa*, are of the June-bearing type (Darrow 1966). June-bearing cultivars are predominantly grown for commercial purposes in the Upper Midwestern United States, where other flowering types have historically performed poorly (Durner *et al.* 1984; Luby *et al.* 1987; Luby 1989). June-bearing cultivars induce flowers under shortening daylengths, optimally from 9.5 to 13-h days, depending on cultivar (Darrow and Waldo 1933). The change in daylength over time in the United States Upper Midwest (specifically using Minneapolis, MN 44.9833° N as a representative point) compared to a more southern latitude, where strawberries are also grown (specifically using Santa Maria, CA 34.5914° N as a representative point), is shown in Fig. 1.5. The figure implies that flower induction would typically occur in mid-September for June-bearing cultivars in the Minneapolis area, until temperatures induce plants into dormancy. Savini *et al.* (2005) noted that June-bearing cultivars will also have flower initials before they enter dormancy. For many June-bearing cultivars the dormancy-inducing temperature is a high of 10 °C (Kronenberg *et al.* 1976). On average, this threshold temperature will be reached in early November in the United States Upper Midwest (Fig. 1.6).

As daylength and temperatures increase the following spring, June-bearing plants stop flower induction and divert resources into flower development (Salisbury and Ross 1992; Nishizawa and Shishido 1998). This induction-to-development shift leads to June-bearing plants bearing high fruit yields until the induced flower buds are depleted, typically in late June or early July. Thus, June-bearing strawberry plants can be considered to have short-day induction requirements

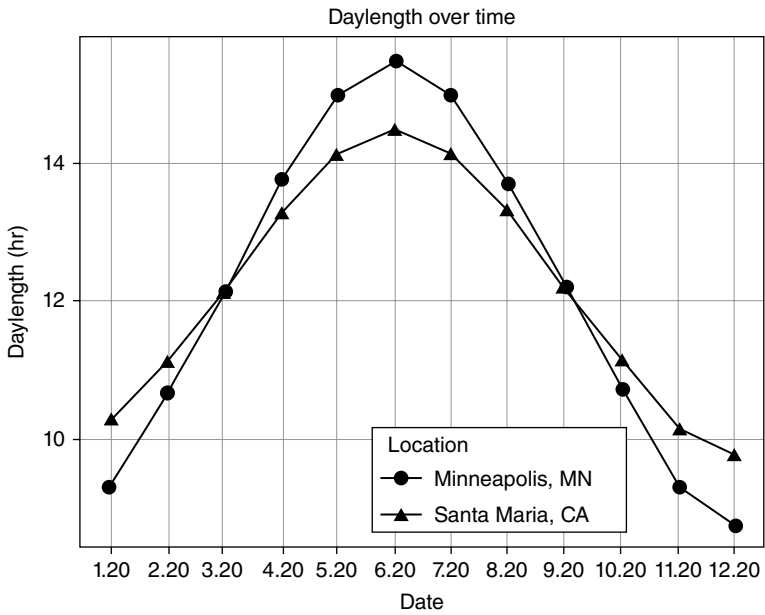


Fig. 1.5. Average daylengths of Minneapolis, MN and Santa Maria, CA, taken on the 20th of each month. Raw data acquired from Time & Date AS: <http://www.timeanddate.com/worldclock/astromy.html?n=3857&month=12&year=2014&obj=sun&afl=-1&day=1>.

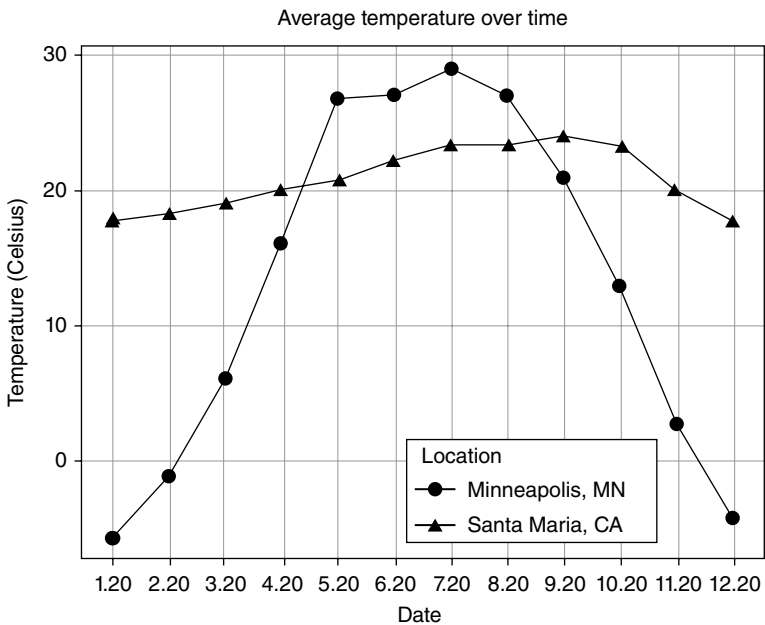


Fig. 1.6. Average high temperatures in Minneapolis, MN and Santa Maria, CA, taken on the 20th of each month. Raw data acquired from Intellicast: <http://www.intellicast.com/>.

and long-day development requirements. Under high temperatures (>30 °C), June-bearing plants will experience severely reduced flower development, even in optimal photoperiods (Serce and Hancock 2005). Savini *et al.* (2005) also noted that the morphology and differentiation time of inflorescences is based on the thermo-photoperiod that the plant is exposed to; June-bearing plants growing in warmer, short-day conditions tend to have faster and more prolific flower differentiation and shorter petiole lengths than plants exposed to long-day, cooler conditions.

Common cultural practices treat June-bearing strawberries as a perennial crop, typically using a “matted row” system. Rooted plugs of the June-bearing crop are planted in the spring of the first year (the “establishment” year). Flower clusters are typically removed during this entire first season, allowing the plant to divert more reserves into crown/branch crown development, root development, and runner production (Eames-Sheavly *et al.* 2003). June-bearing cultivars rarely establish runners during early season flower development. However, both flowering and runnering take place as daylength increases, and finally runners alone are developed during the hottest, longest photoperiods of the summer (Stewart and Folta 2010). Growers often arrange runners spatially from the crown to eventually root themselves, creating a thick, matted row of plants (Fig. 1.7) (Archbold and MacKown 1995). The plants then overwinter, and flower clusters induced during the short daylengths of fall are left on the plant the following spring for the first harvest. In this system, the number of leaves on each plant at the beginning of overwintering can be correlated with fruit production the following year (Poling 2012).

2. Everbearing and Day-neutral. The second and third flowering types, everbearing and day-neutral, are often considered synonymous, likely due to crossover in pedigrees. Everbearing cultivars include the diploid alpine strawberry *F. vesca*, along with various more common octoploids (Duchesne 1766; Fletcher 1917). Cultivars categorized as everbearing both induce and develop flowers under longer photoperiods, typically 12 h or more. Sironval and El Tannir-Lomba (1960) found that flower induction and development of *F. vesca* var. *semperflorens* was inhibited when plants were exposed to short-day treatments. Octoploid everbearing cultivars initiate most of their flowers on unrooted or recently rooted runners during the long days of summer, leading to fall harvests (Stewart and Folta 2010). The origin of the everbearing trait appears to have occurred separately in North America and Europe, as little crossbreeding occurred

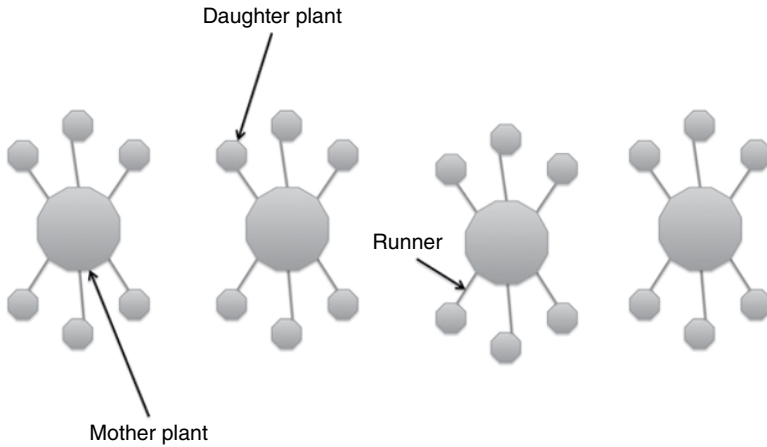


Fig. 1.7. Diagram of the matted-row system common to June-bearing cultivars.

between European everbearing *F. vesca* and North American everbearing *F. virginiana* cultivars (Stewart and Folta 2010). The North American everbearing phenotype is due to a single, unstable locus within the typical June-bearing genome (Stewart and Folta 2010), while the origin of the European everbearing trait is older and more difficult to identify (Darrow 1966).

The first recorded instance of a day-neutral phenotype was *F. virginiana* sub. *glauca*, and this was used as a parent in commercial everbearing breeding programs in the 1930s and 1940s (Darrow 1966). *F. vesca* may also display day-neutrality (Iwata *et al.* 2012). Many everbearing cultivars such as ‘Arapahoe’ and ‘Ogallala’ have day-neutral parents present in their pedigrees, which may contribute to why everbearing and day-neutral cultivars are sometimes thought to be the same (Hildreth and Powers 1941). However, true day-neutral cultivars often exhibit flowering habits that are phenotypically distinct from their everbearing relatives. The crowns of all day-neutral genotypes have a strong tendency to fruit prolifically in their first year, as opposed to most everbearing genotypes (Ahmadi and Bringhurst 1991). Day-neutral runners can also develop inflorescences before rooting occurs (Fig. 1.8). Just as important, day-neutral cultivars are historically documented as insensitive to changing photoperiods, fruiting at the same rate throughout a growing season of dynamic daylength (Durner *et al.* 1984). This distinguishes day-neutral cultivars from everbearing cultivars, which display long-day photoperiodism for flower induction and



Fig. 1.8. Day-neutral 'Monterey' runner, with developed inflorescence. Photograph taken July 10, 2014, in Minnesota.

development. These traits, in addition to increased heat tolerance (Stewart and Folta 2010), have contributed to abundant strawberry production in California, where day-neutral cultivars perform well. Other areas of the United States, such as the Upper Midwest, did not observe the same success, as day-neutral cultivars yielded poorly in Midwestern climates and were difficult to propagate (Durner *et al.* 1984; Luby *et al.* 1987; Luby 1989). This day-neutral market advantage allows California to account for 44% of the total national strawberry acreage and almost 90% of total yields, leading to a total revenue of \$US 2.12 billion in 2012 (California Agric. Statistics Review 2014; National Agric. Statistics Service 2014).

In environments where they are commercially viable, day-neutral phenotypes are typically managed as annual plants in raised-bed systems with drip-tape irrigation and plastic mulch. An abundance of research has been conducted on cultivar/plastic combinations, with the consensus being that year-to-year and environmental variances across sites complicate the development of a single, optimal cultural practice for day-neutral production (Himelrick *et al.* 1992; Hughes *et al.* 2013). Recently, high tunnel structures that increase air and soil temperatures offer season extension potential, and have been shown to increase total

and marketable yields in day-neutral strawberry cultivars without pollination being inhibited by the closed structure (Kadir *et al.* 2006). However, there has been a documented increase in fungal disease incidence in high tunnel systems due to reduced air circulation (Kennedy *et al.* 2013).

It is often considered good horticultural practice to remove flower clusters from June-bearing plants for the first four to six weeks after initial planting (Eames-Sheavly *et al.* 2003); this forces the plants to partition more metabolites into vegetative growth and runner production, making the perennial crop more productive in subsequent years. Flower cluster removal is also practiced in day-neutral production, even though day-neutral cultivars are often only grown as annuals. Interestingly, Lantz *et al.* (2009), when conducting a study in Garrett County, Maryland (39.2833° N), demonstrated no significant difference in total yield when day-neutral ‘Seascape’ plants did not have flower clusters removed compared to treatments where flower clusters were removed two and four weeks after planting.

3. Thermoperiod and Temperature Effects. There is still some uncertainty regarding the photoperiodic nature of June-bearing, ever-bearing and day-neutral flowering habits. While the common consensus is that June-bearing cultivars display short-day flower induction, ever-bearing cultivars display long-day flower induction and day-neutral cultivars are truly photoperiod insensitive, additional research has led many to believe that the photoperiodic tendencies of strawberry cultivars can be altered with temperature (Durner *et al.* 1984; Sonstebly and Heide 2007). In many cases, cultivars classified under photoperiodic categories only display their classified flowering response in moderate temperature conditions; once a certain threshold temperature is exceeded, their photoperiodic nature changes. For example, Guttridge (1985) found that flower induction of certain June-bearing cultivars can occur under any photoperiod if temperatures are <15 °C. Nishiyama and Kanahama (2000) demonstrated that the day-neutral cultivar ‘Hecker’ had inhibited flowering at high temperatures (30 °C/26 °C) when long day lengths (>14 h) were not present. This implies that some day-neutral cultivars may display long-day flowering habits under high-temperature conditions. Indeed, Sonstebly and Heide (2007) found similar results when testing the cultivar ‘Elan’, leading them to conclude that “...everbearing strawberry cultivars, in general, whether of the older European-type or the modern Californian-type originating from crosses with selections of *F. virginiana* ssp. *glauca*, are qualitative (obligatory) LD plants at high temperature (27 °C), and quantitative LD

plants at intermediate temperatures. Only at temperatures below 10 °C are these cultivars day-neutral.”

Such general statements should be avoided, however, since there is considerable variability in strawberry flowering and fruiting response to temperature, even within the June-bearing, everbearing, and day-neutral categories (Wagstaffe 2009). For example, Bradford *et al.* (2010) discovered that plants of the day-neutral cultivar ‘Tribute’ required long photoperiods for flowering after a threshold temperature of 26 °C was exceeded, while plants of the day-neutral cultivar ‘RH-30’ required short photoperiods for flowering once the temperature exceeded 23 °C. This variance of thermo-photoperiod within a flowering category suggests that study is merited on all cultivars of commercial significance, even if research has already been conducted on similar cultivars within their traditional photoperiod classification.

Temperatures can also affect fruit production in ways that are not related to photoperiod. Kumakura and Shishido (1995) observed that strawberry flower buds of everbearing cultivars aborted during periods of high temperature (30 °C), while Karapatzak *et al.* (2012) found that everbearing cultivars exposed to supraoptimal temperatures (30 °C/20 °C) experienced severely reduced pollen viability leading to significantly reduced yields. Similar supraoptimal temperature effects were observed with June-bearing cultivars (Ito and Saito 1962; Durner *et al.* 1984). Yield reductions likely manifest as a result of unviable pollen contributing to poor fertilization and misshapen fruit (Ariza *et al.* 2011). These reductions in pollen viability appear to be dependent on high night temperatures, as supraoptimal day temperatures with cool night temperatures did not result in reduced viability (Wagstaffe 2009). The effect of supraoptimal temperatures on flowering and yield in day-neutral cultivars is less thoroughly researched, though day-neutral cultivars have previously been regarded as being more heat-tolerant (Stewart and Folta 2010).

Suboptimal temperatures can also affect fruit development. Ariza *et al.* (2015) conducted a thorough analysis of cold temperature on differentiating inflorescences, and observed that chilling events (24 h at 2 °C) can reduce pollen grain production and viability as early as 20 days before anthesis, and increase ovule abortion three to six days before anthesis. These events would be especially deleterious for June-bearing plants, as all June-bearing flower buds develop in the spring when chilling events are more likely to occur. A chilling event on day-neutral plants may also inhibit fruit production on developing inflorescences, but since day-neutral plants tend to produce inflorescences throughout the growing season it likely would not have as large an