QUANTIFYING THE INFLUENCE OF PHOTOPERIODIC LIGHTING ON CONTROLLED ENVIRONMENT SPECIALTY CUT FLOWER PRODUCTION

By

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ABSTRACT

Despite increasing demand for new and locally grown specialty cut flowers, protocols for yearround production are limited. An advantage of greenhouse production is the ability to control environmental parameters such as temperature, light intensity, and photoperiod. The implications for commercial production include implementing strategies to hasten or delay flowering to meet market dates. Therefore, our objective was to determine if photoperiod and low temperature influences flower induction and development, time to harvest, yield, and morphology of bluebeard (Caryopteris incana), Billy buttons (Pycnosorus globosus), ranunculus (Ranunculus asiaticus), and dahlia (Dahlia × hybrida). Based on our results, we classified bluebeard as a facultative short-day (SD) plant for flower induction and an obligate SD plant for flower development, and Billy buttons as a day-neutral plant for flower induction and a facultative longday plant for flower development. Growers should provide bluebeard with a 16-h photoperiod or night interruption lighting for 4 to 6 weeks to promote vegetative growth, followed by an 11- to 14-h photoperiod for flower induction and development. A photoperiod ≥ 12 h hastens time to harvest and increases yield and stem quality of Billy buttons. In ranunculus, subsequent flowering was faster following a low-temperature treatment. To ensure marketable stem length, ranunculus should be finished under a 12-h photoperiod. Time to flower and stem length of dahlia was influenced by the duration of photoinductive short-day cycles. As few as 5 and 10 photoinductive SD cycles provided to dahlias can ensure a timely harvest and marketable stem lengths. Our results indicate that photoperiod influences flower induction of all specialty cut flower species investigated, and that controlling photoperiod can hasten flowering and improve flower quality and yield.

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CHAPTER 1

Literature Review: Enhancing controlled environment specialty cut flower production through manipulation of environmental parameters Literature Review: Enhancing controlled environment specialty cut flower production through manipulation of environmental parameters

Introduction

The commercial cut flower industry boasts centuries-old history, contributing substantially to many countries' agricultural economy. There are crops long known for their symbolism amongst nations traditions and customs that are still in place today. Today's global leaders in cut flower exports include the Netherlands, followed by Colombia, Ecuador, Kenya, and Ethiopia (Faust and Dole, 2021). Due to their ideal year-round climatic conditions and lower labor, greenhouse, and production costs, countries near the equator became successful producers of traditional cut flowers in the 1980s (Mendez, 1991; Faust and Dole, 2021). The most common traditional cuts include carnations (*Dianthus caryophyllus*), chrysanthemums (*Chrysanthemum ×morifolium*), and roses (*Rosa* spp.) (Gast and Stevens, 1993; Xia et al., 2006) and they are typically mass produced in large farms. Today, export sales and earnings for cut flowers continue to increase around the world. For example, the Colombian annual cut flower export value has steadily increased from \$0.6 billion in 2000 to upwards of \$1.4 billion in 2018 (Faust and Dole, 2021).

While the United States (U.S.) is a net importer of cut flowers; there has been a recent resurgence of domestic cut flower production (Loyola et al., 2019). In 2022, the wholesale value of domestically grown cuts rose to \$333.1 million, marking an increase from the \$295 million reported in 2020 (USDA, 2021; USDA NASS, 2023). California largely dominates domestic cut flower wholesale production, and generated 69% of wholesale value in 2020, amounting to \$203 million (USDA, 2021).

In recent years, the U.S. and Canadian cut flower market has shifted from a predominantly traditional cut flowers to a more diverse market, with an increased demand for

specialty cut flowers. Specialty cut flowers refer to nontraditional crops such as anemone (*Anemone coronaria* L.), gomphrena (*Gomphrena globosa* L.), ranunculus (*Ranunculus asiaticus* L.), and rudbeckia (*Rudbeckia hirta* L.) (Armitage, 1993; Darras, 2020). The classification of specialty cut flowers is loosely defined as there are many cut flowers that could be considered 'specialty'. Darras (2020) described specialty cut flowers as annual or perennial species that are seasonally and locally produced in smaller quantities, have a short post-harvest life, are generally produced outdoors, and often sold to local markets (Darras, 2021). Seasonal, outdoor production is a general characterization of specialty cut flower production, but as demand increases in North America, growers are interested in year-round greenhouse production to meet the growing demand for locally produced cuts and avoid the risks that accompany extreme weather and limited environmental control in high tunnels (Ortiz et al., 2012; Owen et al., 2016; Darras, 2020).

Due to the extensive selection of specialty cut flowers available, growers can produce them throughout the natural growing season in temperate regions by strategically growing crops that flower in the spring, summer, and fall. Based on the time of year, the cut flower market can become saturated with certain flowers that are in season. For example, a farmers' market in the Midwest in April and May can expect to offer many early blooming crops such as iris (*Iris* ×*germanica*) and tulips (*Tulipa* spp.). However, the August and September market is often filled with varieties of dahlia (*Dahlia* spp.), gladiolus (*Gladiolus* spp.), marigold (*Tagetes erecta*), sunflower (*Helianthus annus*), and zinnia (*Zinnia elegans*) (Bachmann, 2006). By aligning their cut flower portfolio with the inherent growing season of crops, growers can have a steady source of flowers and income.

There are also seasons in which cut flower sales typically spike in response to cultural

gift-giving occasions. Increases in cut flower purchases tend to occur around holidays such as Valentine's Day, Christmas, Easter, and Mother's Day. Valentine's Day accounts for 30% of all holiday-related floral purchases each year, followed by Christmas and Mother's Day accounting for 26% each (Society of American Florists, 2018). However, not all cut flower transactions are made during holiday seasons — weddings, anniversaries, birthdays, funerals, as well as for personal enjoyment are driving factors for purchases. Cut flowers can represent symbols of love, sympathy, apology, and appreciation and possess a set of aesthetic attributes that are associated to the occasion of purchase (Yue and Hall, 2010). In addition to the symbolism behind purchasing and gifting cut flowers, there is also a loose cultural consensus as to what flower colors represent and how they may convey different expressions of emotion, further influencing a consumer's purchase (Yue and Behe, 2010). The significance of color can influence the choices made by growers, shaping their decisions on which flowers and varieties to cultivate in order to effectively target particular markets. Ultimately, the cut flower market is driven by lifestyle choices that are traditionally integrated into society (Xia et al., 2006).

The Association of Specialty Cut Flower Growers (ASCFG), for example, has seen a notable rise in membership. From 1996 through 2014, the organization was comprised of around 500 members and as of 2018, membership has risen to 1,700 (Loyola et al., 2019). As the production of specialty cut flowers is a relatively recent transition, it is only natural that certain growing and postharvest challenges have arisen, impacting both the quality and overall yield for growers. For example, a 2019 survey of ASCFG members was launched to identify the most prevalent production and postharvest problems facing specialty cut flower growers in the United States and Canada (Loyola et al., 2019). According to the survey, the primary production challenges were crop timing and insect and disease management. Additional problems reported

were nutrient and water management and labor availability (Loyola et al., 2019).

Production of Cut Flowers

In North America, cut flowers are predominately produced outdoors in fields and high tunnels, with a growing number of operations utilizing greenhouses for additional environmental control for year-round production (Ortiz et al., 2012; Owen et al., 2016; Nobes et al., 2021). There are advantages and disadvantages for each of the above-mentioned production systems, and the selection is based on growers' geographic location, prevailing climate, economic feasibility, and the marketability of the specific crop during different seasons.

Field production of cut flowers avoids the initial investment in infrastructure and continued operating and energy costs needed for greenhouse production (Starman et al., 1995). However, open field production can be heavily impacted by extreme weather events and, depending on the location, production of cut flowers may only be achievable seasonally when plants flower naturally (Kelly, 1991). The inability to implement significant season extension in high tunnels reduces the potential for reaching markets early or later, limiting the potential for increased profitability (Nobes et al., 2021). Nonetheless, year-round field production of cut flowers is achievable in some regions of the U.S., that include Hawaii, Florida, and California due to their year-round favorable climate (Nobes et al., 2021).

High tunnel production is in between open field and greenhouse production. Structurally, high tunnels are composed of a frame made of pipe or tubing and are typically covered with a single layer of 6-mil polyethylene film (Carey et al., 2009). They are not highly mechanized and therefore do not have the ability to control the environment; however, they can be passively ventilated and can contain irrigation systems (Carey et al., 2009). High tunnels are utilized for season extension function to protect crops from undesired environmental conditions (Lamont,

2009). In northern latitudes, for example, high tunnels offer protection from frost and low temperatures and can extend the growing season during the spring and fall by several weeks (Wien and Pritts, 2008). Protection from wind and precipitation in combination with controlled irrigation methods such as drip irrigation help minimize potential disease incidence and increase stem quality (Lamont, 2009; Ortiz et al., 2012).

Crops commonly grown in high tunnels include vegetables, small fruit, tree fruit, and cut flowers (Lamont, 2009). In high tunnels, the daily light integral (DLI) is generally lower compared to in the field. Cut flowers tend to produce longer stems in high tunnels, primarily because of the reduced DLI and limited air movement (Ortiz et al., 2012).

Compared to field and high tunnel systems, greenhouse production of cut flowers provides the greatest level of environmental control, such as the ability to maintain day and night air temperatures, DLIs, photoperiods, and humidity. They often provide greater predictability of crop timing and quality due to the heightened control of the crop growing environment. Additionally, greenhouse production allows for scheduling and sequential plantings to meet specific market dates (Nobes et al., 2021). For example, Nobes et al. (2021) compared time to harvest of various cut flower varieties when grown in high tunnels and greenhouses. Generally, the number of days to harvest was lower when grown in a greenhouse, which allows for earlier marketability and reduced labor costs (Nobes et al., 2021; Ortiz et al., 2012).

Photoperiod, temperature

As previously mentioned, manipulation of environmental parameters is advantageous for cut flower growers to meet pre-determined market dates. Temperature regulates plant growth and development and can be considered a signal for developmental processes such as time to flower and harvest (Franklin and Wigge, 2013).

Due to the increased demand for specialty cut flowers, it is of interest to investigate how temperature influences emergence, developmental parameters, and quality of cut flowers. For example, *Ranunculus asicaticus*, is a high-value cool-season specialty cut flower that is native to Mediterranean regions in southwestern Asia and southeastern Europe characterized by hot, dry summers and cool, wet winters (Beruto et al., 2018). Ranunculus cut flower growers located in northern latitudes typically begin planting tuberous roots in the fall to expose them to cool temperatures. This mimics the cool winter and early spring flowering that they experience naturally. Similarly, ranunculus is marketed in North America as an early spring cut flower and are popular in wedding and spring arrangements (Rauter and Stock, 2023). They are sensitive to temperatures above 26 °C as flower production is inhibited (Rauter and Stock, 2023).

In their native habitat, plants with underground storage organs known as geophytes, will sprout after rain rehydrates the previously dormant storage organ (Meynet, 1993). This rehydration occurs in the fall, while the winter months are when the plant experiences vernalization. During this cold period, most bulbs require a temperature of 4 to 9 °C for the promotion of shoots and anthesis in the spring (Khodorova and Boitel-Conti, 2013). Ranunculus will begin to develop a rosette of petiole leaves and plants will produce flowers from February to May. As temperatures exceed optimal growing conditions in the summer months, the plant will enter dormancy and the vegetative growth will die back (Horovitz, 1985; Meynet, 1993). Therefore, ranunculus and other spring flowering geophytes require exposure to a warm-coldwarm sequence to promote active vegetative and reproductive growth (Le Nard and De Hertogh, 1993).

For ranunculus production, dry tuberous roots or rhizomes are soaked in aerated water for 3 to 36 h to rehydrate prior to planting (Ohkawa, 1986; Meynet, 1993). Following rehydration, it

is suggested that tuberous roots are pre-sprouted, which involves transplanting them in growing medium at cool temperatures for multiple weeks (Horovitz, 1985; Armitage, 1993). This is said to hastened flowering compared to direct planting of and a two-week pre-sprout period is sufficient to develop visible roots and shoots at the time of planting (Faust and Dole, 2021). These methods have been reported to successfully maximize the overall quality, grade, yield and profitability. Rauter et al. (2022) found that a two-week pre-sprout period hastened time to harvest up to one week compared to tuberous roots that were directly planted and it improved yield under high tunnel and spring field plantings. Likewise, anemone (*Anemone coronaria*) is another tuberous roots cut flower species that benefits from pre-sprouting procedures consisting of rehydrating tuberous roots and transplanting into trays for three to four weeks at 2 to 5 °C to ultimately reduce time in the greenhouse and accelerate flowering (Hertogh, 1996).

Another method used to force flower bulbs into flower is vernalization. Vernalization is a process necessary for predominately spring-flowering bulb species that entails exposing them to prolonged cold temperatures and moisture for a species-specific time to ensure quality flowering (Chouard, 1960). Although there are multiple environmental factors (ie. light, moisture, temperature) that affect bulb development, it has been recognized that temperature plays a predominant role in regulating growth and flowering in bulb species (Le Nard and De Hertogh, 1993; Khodorova and Boitel-Conti, 2013). The low temperature accumulation necessary for vernalization stimulates cascades of developmental mechanisms and flowering pathways to achieve flowering and vegetative reproduction (Ben Michael et al., 2020).

Many lily species, for example, also benefit from vernalization to accelerate shoot emergence and flowering. Optimum vernalization conditions, however, vary from species to species. Lee et al. (1996) investigated the effect of bulb vernalization duration on Asiatic hybrid

lily (*Lilium* ×*elegans*) and reported that storage \geq 4 weeks at 5 °C was necessary to hasten flowering in three selected lines of Asiatic hybrid lilies that varied in flowering time (i.e. lateseason, mid-season, or early-season flowering). For all three lines, shoot emergence was delayed when bulbs were vernalized for 0 and 2 weeks compared to those vernalized for \geq 4 weeks. The number of days to shoot emergence was delayed by 119, 25, and 17 d for Lines A, B and C, respectively. Time to flower in all three lines showed similar trends to shoot emergence (Lee et al., 1996).

Ranunculus flowering is also influenced by the temperature the tuberous root has experienced as well as the photoperiod during plant growth (Carillo et al., 2020). Photoperiodism is a plant's response to changes in the daylength that enables adaptation to seasonal changes in the environment (Thomas and Vince-Prue, 1997); however, it is the length of the dark period that plants perceive to determine seasonal changes in their environment (Faust, 2011). The natural photoperiod shifts due to the tilt of the earth's axis and its annual rotation; daylengths become longer in the summer and shorter in the winter (Jackson, 2009). Changes in daylength provide environmental signals that are indicative of the time of year, which can coincide with many developmental responses (Thomas and Vince-Prue, 1997; Jackson, 2009). For plants, developmental processes that are influenced by photoperiod include tuberization, dormancy, and most commonly flowering (Faust, 2011).

It has been thoroughly documented that developmental processes such as flowering are influenced by photoperiod, with some responses accelerated by growing certain plants under long days (LDs) or short days (SDs) (Thomas and Vince-Prue, 1997). Short-day plants (SDPs) experience an accelerated flowering process when grown under daylengths that are shorter than a critical daylength, while long-day plants (LDPs) exhibit accelerated flowering when grown under

daylengths exceeding a critical daylength (Faust, 2011). Not all plants, however, can be considered SDPs or LDPs — day-neutral plants initiate flowering irrespective of daylength, such as impatiens (*Impatiens hawkeri*) (Faust, 2011).

A plant's flowering response to daylength can be further classified as facultative or obligate. Plants classified as having an obligate response absolutely require a particular photoperiod to flower (Faust, 2011). For example, obligate SDPs will only flower when exposed to SD conditions and will remain vegetative under LDs. Obligate SDPs include chrysanthemum (*Chrysanthemum morifolium*) and poinsettia (*Euphorbia pulcherrima*) (Runkle et al., 2017). Conversely, obligate LDPs, will only flower in response to LDs. There are many herbaceous perennials that are considered obligate LDPs such as campanula (*Campanula carpatica*) (Runkle et al., 2017). Additionally, a plant can be classified as having a facultative response if they flower faster under a specific photoperiod but eventually flower under all photoperiods (Faust, 2011). Petunia (*Petunia* ×hybrida), for instance, is considered a facultative LDP — time to flower is shortest under LD conditions, but flowering will eventually occur under SDs (Thomas and Vince-Prue, 1997).

One of the advantages of greenhouse production is the ability to manipulate environmental parameters. In the field or in a high tunnel, plants flower in response to the natural daylength. In a greenhouse, growers can manipulate the natural photoperiod to create artificial LDs or SDs (Runkle, 2003). Short days can be created by pulling opaque black cloth or plastic at the beginning or end of the day under natural LD conditions (Runkle, 2003). This process, however, is often labor intensive.

Dahlias (*Dahlia* spp.) are classified as facultative short-day plants (SDPs), generally flowering from late summer into early fall as the days shorten. Cut flower production for dahlias

typically occurs outdoors and continues until the first frost of the season. Due to their response to day length and sensitivity to frost, dahlia production is highly seasonal and therefore limited. Given the high demand for dahlias as a specialty cut flower, growers could benefit from greenhouse production, where the use of black cloth, temperature, photoperiodic lighting can be manipulated to extend the growing season.

Under natural SD conditions, providing photoperiodic lighting at the end of the day or during the middle of the night extends the daylength by reducing or interrupting the dark period, therefore creating LD conditions (Runkle, 2003). Night interruption (NI) lighting is a strategy used to break up the long dark period, rather than extending the photoperiod at the end of the SD (Vince-Prue and Canhan, 1983). A NI break typically takes place for 4 h from 2200 to 0200 HR, which creates two 6 h periods of darkness that will either inhibit flower induction for SDPs or promote flower induction for LDPs (Park and Jeong, 2020). It only takes a photon flux density (*PPF*) around 2 μ mol·m⁻²·s⁻¹ of light for plants to perceive daylength. At this low light intensity, a plant's photoreceptors can detect light quality and absorb red (R), far-red (FR), and blue light. (Runkle and Heins, 2001).

Phytochromes are plant photoreceptors that primarily absorb peaks in the red (R; 600-700 nm) and far-red (FR; 700-800 nm) spectrum (Sager et al., 1988; Craig and Runkle, 2012). Phytochromes respond to the radiation they are exposed to and are present in two interconvertible forms, the R-radiation-absorbing form Pr and FR-absorbing form Pfr. Upon absorbing R light, Pr converts to Pfr, which then converts back to Pr upon absorbing FR light or during dark periods (Sager et al., 1988; Thomas and Vince-Prue, 1997). Pr is denoted as the "inactive" conformation, while Pfr is the "active" conformation of phytochrome (Runkle and Heins, 2001; Craige and Runkle, 2012).

phytochrome photoequilibrium (PPE), which is the current amount of P_{fr} relative to both P_r and P_{fr} (P_{fr}/P_{r+fr}); Craig and Runkle, 2016). Flowering is promoted in LDPs when there are sufficient concentrations of P_{fr} in relation to the total phytochrome, or a high PPE; conversely, SDP flowering is promoted when PPE is low due to low relative P_{fr} concentrations (Craig and Runkle, 2016). For example, the prolonged light exposure under LDs induces greater P_{fr} concentrations, while the short nights prevent mass conversion back to P_r , increasing the PPE and inducing LDP flowering. SDs, on the other hand, induce P_{fr} gradually converting to P_r during long dark periods, lowering the PPE and promoting flowering in SDPs. Growers will often interrupt a long night with light for 2 hours or more to effectively interrupt the P_{fr} to P_r conversion (Craig and Runkle, 2016). This night-interruption (NI) strategy successfully promotes flowering in LDPs due to the excess P_{fr} that is left over from the interrupted conversion.

NI lighting can also be used to inhibit flowering of SDPs. Craig and Runkle (2013) reported that a R:FR ratio of 0.66 or greater is effective at interrupting a long night and promotes stem elongation and reduced flowering in Chrysanthemum (*Chrysanthemum morifolium*), dahlia (*Dahlia hortensis*), and African marigold (*Tagetes erecta*). These SDPs were grown under a 9-h SD with or without a 4-hour NI using incandescent lamps or light-emitting diodes (LEDs) with several different R:FR ratios. Flowering in chrysanthemum was not inhibited under a R:FR ratio of 0.28 or lower but flowering percentage was reduced under a R:FR ratio of 0.66 or higher. Dahlia and African marigold flowering demonstrated varying responses to NI treatments, and it was reported that for all species, stem length increased as the R:FR ratio of NI treatment increased (Craig and Runkle, 2013). NI lighting can be utilized as a tool to regulate flowering in both LDPs and SDPs, however, ornamental flowering species all have a varying sensitivity to R:FR ratios, meaning that light quality and quantity may require manipulation to achieve the

desired effect on flower regulation and stem elongation.

For some plants, there is an interaction between the critical photoperiod and the number of inductive cycles that a plant will receive. Flower induction occurs as the result of an integration of environmental signals, such as photoperiod and vernalization (Kobayashi and Weigel, 2007). An inductive photoperiod can be defined as the exposure of mature plants to at least a minimum number of appropriate day/night length cycles that results in the accumulation of flower signals perceived by leaves (Warner, 2009). To determine the minimum number of day/night length cycles required for flower induction resulting in floral initiation, limited inductive photoperiod transfer experiments can be performed where plants are exposed to various inductive photoperiod cycle treatments before being grown under noninductive conditions (Damann and Lyons, 1993). Warner (2009) investigated how many SD photoinductive cycles celosia (Celosia argenta L. var. Plumosa Voss), a facultative SD plant, required for floral induction. It was suggested that ~6 to 9 SDs were necessary for plants to be receptive and induce flowering, depending on the cultivar tested. Plants that showed early flower induction and early flowering produced fewer inflorescences, lateral branches, and shoot dry weight. These results are supported by Verheul et al. (2006), who suggested that there is often a quantitative relationship between the number of inductive photoperiods received and the strength of the flowering response (i.e. number of inflorescences produced, and number of flowers produced per inflorescence). This information is useful for commercial production because it can be applied to crop scheduling to determine a crops' time to flower for marketability purposes, and it improves the overall crop quality.

The light environment largely contributes to the flower induction and development of a plant, however, interactions with temperature can also influence growth and flowering. The

critical photoperiod can vary with temperature. Brøndum and Heins (1993) investigated how the morphological development and growth rate of *Dahlia pinnata* was influenced by temperature and photoperiod. Plants were exposed to temperatures of 15 to 30 °C and 6 different photoperiods to produce twenty-four factorial temperature ´ photoperiod treatments. It was found that lower temperatures and SD photoperiods encouraged tuber root formation in dahlia, which supported previous research findings. Primary shoot length, lateral shoot length, and node count was also affected by temperature and photoperiod (Brcøndum and Heins, 1993). In summary, temperature and light both significantly influence a plant's growth and development; however, it is the interaction between both parameters that can have the most effective influence on development of plants for regulation of flowering.

Conclusion

The specialty cut flower market continues to grow in North America; however, yearround production may only be feasible in some regions due to unfavorable climate conditions in northern latitudes during the winter season. To avoid seasonal production, growers are interested in controlled-environment greenhouse production to provide optimal environmental conditions year-round. To optimize greenhouse production, further information is necessary regarding flower forcing conditions for many species of specialty cut flowers. Day length is a largely influential environmental signal for flower initiation and development and further research would be advantageous for growers to determine the critical photoperiod of new crops. Application of this information would allow growers to increase yield and quality of their product and benefit economically from the increasing demand for domestically sourced cut flowers.

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CHAPTER 2

Daylength influences time to harvest and stem quality of *Pycnosorus globosus* and *Caryopteris incana* specialty cut flowers

Daylength influences time to harvest and stem quality of *Pycnosorus globosus* and *Caryopteris incana* specialty cut flowers

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Abstract

As the demand for locally grown specialty cut flowers increases, varieties of *Pycnosorus* globosus and Caryotperis incana are becoming more available for growers to produce as cuts. However, protocols for year-round greenhouse production are limited. Therefore, our objective was to determine if photoperiod influences flower induction and development, time to harvest, yield, and morphology of billy buttons (Pycnosorus globosus) 'Paintball Globe' and 'Paintball Poppy' and bluebeard (Caryopteris incana) 'Pagoda Lagoon' and 'Pagoda Dark Pink' to facilitate commercial greenhouse production. Shoot-tip cuttings were rooted and transplanted into bulb crates and placed in a greenhouse with a mean daily air temperature of 20 °C and under 9-, 10-, 11-, 12-, 13-, 14-, 15-, or 16-h photoperiods or a 9-h short day (SD) with a 4-h night interruption (NI) from 2200 to 0200 HR for 11 weeks. Billy buttons initiated inflorescences and developed flowers under all daylengths; however, the greatest stem lengths were recorded under long days (LD). Bluebeard inflorescences initiated under all daylengths tested. Time to visible inflorescence and flower was hastened under daylengths ≤ 14 -h, while inflorescences under the 16-h photoperiod or 4-h NI never fully developed. For 'Pagoda Lagoon' and 'Pagoda Dark Pink', the critical daylength for flower development was 14 and 15 h, respectively. On average, only bluebeard 'Pagoda Lagoon' harvested under photoperiods ≥10 h developed marketable stem lengths (>40 cm). To hasten time to visible inflorescence and harvest and ensure marketable stem lengths, billy buttons should be grown under daylengths ≥ 13 h. Based on these results, we recommend growing bluebeard under a 16-h photoperiod or NI for 4 to 6 weeks to promote vegetative growth, followed by an 11- to 14-h photoperiod for flower induction and development. We classify billy buttons as a day-neutral plant for flower induction and a facultative LD plant for flower development. Similarly, bluebeard can be classified as a

facultative SD plant for flower induction and an obligate SD plant for flower development.

Keywords: *Caryopteris*, *Craspedia*, flower induction and development, night interruption, photoperiodic lighting, *Pycnosorus*

Abbreviations: B, blue; DLI, daily light integral; FR, far-red; G, green; LD, long-day; LDP, long-day plant; LED, light-emitting diode; MDT, mean daily temperature; NI, night-interruption; R, red; SD, short-day; SDP, short-day plant; TH, time to harvest; TVI, time to visible inflorescence; VI, visible inflorescence

Introduction

In contrast to traditional cut flowers such as rose, carnation, and chrysanthemum imported year-round from equatorial countries, specialty cut flowers are produced seasonally in North America. This results in limited quantities of specialty cut flowers being available to local markets (Darras 2021). These cut flowers are generally only available during times of the year when they naturally flower without environmental manipulation. While traditional cut flower production remains cost-effective in South America and Africa, successful domestic production of specialty cut flowers in North America is achievable by specializing in unique, high-value, crops that perform poorly during long-distance shipping. Greenhouse production of cut flowers is a potential solution for season extension and improvement of cut flower yield and quality in temperate regions; however, the construction and maintenance expenses limit this production method for many small growers (Ford et al. 2012). Greenhouse production enables growers to shift from seasonal cultivation to a more continuous, year-round schedule and meet predetermined market dates throughout all seasons.

Billy buttons (*Pycnosorus globosus*), also known as billy balls, drumstick flower, woollyheads, and previously referred to as *Craspedia globosa*, is native to the Australian continent that was introduced and bred as a specialty cut flower due to its cultivation success as a floriculture crop (Johnston and Joyce, 2007; Darras, 2020). In North America, it is traditionally marketed as an annual bedding plant; however, it is a perennial in United States Department of Agriculture hardiness zones 8 to 11. Native to eastern regions of New South Wales, Australia, it grows in temperate and coastal climates where they flower throughout the spring and summer.

Similar to other plants in the Asteraceae family, billy buttons are associated with a distinctive head-like inflorescence, known as a capitulum. A capitulum mimics a single flower

but is a highly amassed structure comprising many flowers with specialized functions (Elomaa et al., 2018). Each billy button stem has one bright yellow capitulum and is often used as bouquet fillers throughout the cut flower market. Its unique morphology as both a fresh and dry cut flower adds to its appeal.

Annis et al. (1992) investigated the influence of photoperiod and exogenously applied gibberellin on vegetative and floral development of billy buttons. Plants were grown under an 11-h short day (SD) or a long day (LD) that consisted of a 4-h night-interruption (NI). Gibberellin was applied as a foliar spray weekly at 0 and 500 mg·L for 0, 5, or 10 weeks. They reported cut flower yield increased from 0.3 to 7.5 stems when plants were grown under SDs and LDs, respectively. Under LD conditions, flower induction [i.e. visible inflorescences (VI)] and anthesis occurred more rapidly, reducing time to VI from 113 d under SD to 93 d under LD conditions. Gibberellin application did not reduce time to harvest or increase flower yield; therefore, it is not a replacement for LDs (Annis et al., 1992). Similarly, flower induction of Shasta daisy (*Chrysanthemum* ×*superbum*) and Australian strawflower (*Helipterum roseum*), which are members of the Asteraceae family, were hastened under LDs (Griffin and Carpenter, 1964; Sharman et al., 1989).

Specialty cut flowers can also include cultivated woody perennial species that have been hybridized to produce new cut flower varieties (Darras, 2021). Bluebeard (*Caryopteris incana*), also known as blue spirea, is a deciduous perennial shrub that has been used as a specialty cut flower. Native to eastern Asia, it produces violet blue and pink flowers that bloom from late summer into fall. Morphologically, the flowers are composed of dense axillary cymes, where the oldest flower terminates the main axis (Cantino et al., 1998).

While some studies have been conducted to determine the mechanisms that regulate flower induction and development of bluebeard, its specific critical daylength has not been reported. Piringer et al. (1963) investigated the effects of photoperiod, light quality, and temperature on growth and flower induction and development of *Caryopteris* ×*cladonensis*. Plants were grown under an 8-, 12-, 14-, or 16-h photoperiod, or a 3-h NI depending on the study. Stems were longer under extended daylengths, growing to 63, 77, 91, and 95 cm under 8-, 12-, 16-h photoperiods and NI, respectively. Similarly, time to anthesis was influenced by photoperiod; anthesis under 8-, 10-, and 14-h photoperiods occurred after 25, 25, and 30 d, respectively, while anthesis did not occur under the 16-h photoperiod. Piringer et al. (1963) suggested that flower development was influenced by the length of the dark period, and complete development would occur only when the dark period was >8 h.

Similarly, Armitage and Son (1992) grew bluebeard under comparable daylengths. After 11 weeks, plants under the 16-h photoperiod did not produce Vis. Plants grown under the 8- and 12-h photoperiod reached anthesis after 42 and 53 days, respectively. Therefore, bluebeard could be characterized as a facultative SD plant (SDP). Although this information is significant for characterization of bluebeard in response to photoperiodism, more in-depth studies are necessary to determine the critical daylengths for flower induction and development of new varieties and to characterize the correlation between flowering and stem length of bluebeard when grown under various daylengths from 9- to 16-h.

As the interest in year-round greenhouse specialty cut flower production grows, there is an opportunity for growers to effectively manipulate environmental factors such as temperature and light quantity, quality, and daylength to produce additional high-value crops such as bluebeard and billy buttons. However, there is limited information on how environmental

parameters influence flower induction and development of promising cut flower genera. Therefore, the objective of this study was to quantify how day length influences floral induction and development, time to harvest, and floral morphology of billy buttons and bluebeard cut flower varieties.

Materials and Methods

On 04 Oct. 2022 (Rep. 1) and 17 Aug. 2023 (Rep. 2), shoot-tip cuttings of billy buttons 'Paintball Globe' and 'Paintball Poppy' and bluebeard 'Pagoda Lagoon' and 'Pagoda Dark Pink' were received from a commercial breeder (Danziger, Tel Aviv-Yafo, Israel). These varieties were selected as they are emerging specialty cut flowers that have limited information on how daylength influences flower induction and development. Cuttings were inserted into 72-cell trays filled with a 50:50 (v/v) commercial soilless medium [composed of 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products Inc., Galesburg, MI)] and course perlite.

Young plant greenhouse environment

The trays were placed in a glass-glazed greenhouse in the Plant Science Research Greenhouses at Michigan State University (lat. 43°N). Environmental conditions, mist, and fertility followed established propagation protocols (Kohler and Lopez, 2021). An environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada) operated exhaust fans, ridge vents, and radiant steam heating. Substrate temperatures were maintained with bench top root-zone heating and steam was injected to control the vaporpressure deficit. Overhead mist provided 60 mg·L⁻¹ nitrogen as a function of time and accumulated light intensity. The actual air mean daily temperature (MDT), substrate temperature, and vapor pressure deficit over both replications were 21.3 ± 1.3 °C (mean \pm SD), 23.3 ± 1.4 °C,

and 0.4 kPa, respectively. From 0600 to 2200 HR, supplemental lighting from high-intensity LED fixtures (Philips GreenPower LED TopLighting; Philips, Eindhoven, the Netherlands) delivered a total photon flux density of $120 \pm 21 \,\mu$ mol·m⁻²·s⁻¹ [as measured with a quantum sensor (LI-250A light meter; LI-COR Biosciences)] at plant height when the outdoor photosynthetic photon flux density was below \approx 440 μ mol·m⁻²·s⁻¹ to create a 16-h photoperiod. The 100-nm waveband ratios (%) emitted by the LED fixtures, defined by their blue (B; 400-500 nm), green (G; 500-600 nm), red (R; 600-700 nm), and far-red (FR; 700-800 nm) photon flux densities, were 10:6:83:1. A mean daily light integral (DLI) of 5.2 ± 0.3 and $12.5 \pm 1.1 \,\text{mol·m}^{-2} \cdot \text{d}^{-1}$ was delivered for 5 to 7 d of callusing and 21 d of rooting, respectively, during the two replications. *Vegetative growth greenhouse environment*

Billy buttons rooted cuttings were transferred into a greenhouse for two weeks with a 12h photoperiod, and an actual air MDT and DLI of 21.3 ± 0.6 °C and 13.3 ± 3.4 mol·m⁻²·d⁻¹, respectively. They were transplanted into the above-mentioned crates spaced with 20-cm centers at a density of 26 plants per m².

Trays of bluebeard rooted cuttings were transferred into a greenhouse compartment with a 16-h photoperiod created as previously described, and an actual air MDT and DLI of 21.3 ± 0.9 °C and $14.4 \pm 1.2 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, respectively. They were transplanted into 11-cm (600-mL) round containers and then into bulb crates (39.3 cm wide × 59.7 cm long × 17.8 cm tall; 0.23 m²) filled with the above-mentioned commercial medium (Suremix) after 4 weeks. The plants were spaced with 28-cm centers at a density of 17 plants per m².

Flowering greenhouse environment and culture

On 06 Dec. and 13 Dec. 2022 (Rep. 1) and 20 Oct. and 27 Oct. 2023 (Rep. 2), crates containing vegetative billy buttons or bluebeard plants, respectively, were placed under

photoperiod treatments. The treatments consisted of 9-, 10-, 11-, 12-, 13-, 14-, 15-, or 16-h photoperiods or a 4-h NI from 2200 to 0200 HR created with a natural 9 h daylength (0800 to 1700 HR) extended with 13-W GreenPower LED flowering lamp 2.0s (Deep Red/White/Far-red; Signify N.V., Eindhoven, the Netherlands) on each bench. Each LED lamp was covered with two to three layers of aluminum wire mesh (General purpose aluminum; New York Wire, Grand Island, NY) to achieve an average photon flux density of 2 to 3 µmol·m⁻²·s⁻¹ between 400 and 800 nm. The 100-nm waveband ratios (%) emitted by the LED lamps, defined by their B, G, R, and far-red (FR; 700-800 nm) photon flux densities, were 8:13:35:44. The spectral distributions of the LED lamps were measured in six random locations throughout each bench with a spectroradiometer (LI-180; LI-COR Biosciences, Lincoln, NE), and the phytochrome photoequilibrium was estimated to be 0.66 according to Sager et al. (1988). The same highintensity LED fixtures described above provided a supplemental total photon flux density of 125 \pm 13 µmol·m⁻²·s⁻¹ from 0800 to 1700 HR. Quantum sensors (LI-190R, LI-COR, Lincoln, NE) or line quantum sensors (LI-191R, LI-COR, Lincoln, NE) were positioned horizontally at plant height on each bench and measured the photon flux densities every 30 s and a datalogger (CR1000X; Campbell Scientific, Logan, UT) recorded hourly averages. The actual DLIs on each bench during the two replications of the experiment are provided in Table 1.

The greenhouse air ADT setpoint was 20 °C (12 h day/ 12 h night of 22/18 °C), with daytime and nighttime temperatures maintained from 0500 to 1700 HR and 1701 to 0499 HR, respectively. An aspirated thermocouple [20-gauge (0.095 x 0.151 mm) type E, Omega Engineering, Stamford, CT] positioned in the middle of each bench measured the canopy air temperature every 30 s, and a data logger recorded hourly means. When the nighttime temperature was <17 °C, the data logger controlled a 1500-W electric heater underneath each

bench to provide supplemental heat. The actual canopy air MDT and mean day and nighttime temperature of each treatment during the finishing stages of the two replications of the experiment are provided in Table 1.

Plants were irrigated with Michigan State University Orchid Reverse Osmosis Special [13N-3P-15K water-soluble fertilizer at a concentration of $(mg \cdot L^{-1})$ 125 nitrogen, 13 phosphorus, 121 potassium, 76 calcium, 19 magnesium, 1.7 iron, 0.4 copper and zinc, 0.9 manganese, 0.2 boron, and 0.2 molybdenum; (GreenCare Fertilizers Inc.)] blended with reverse osmosis water. Two layers of 15 cm supportive netting (HGN32804; Hydrofarm, Petaluma, CA) were secured \approx 30 and \approx 60 cm above the crates.

Data collection and analysis

Each billy button and bluebeard plant per treatment were monitored daily for the presence of the first VI. The date and number of nodes below the first VI was recorded. Individual stems were observed for any open flowers and the date was recorded. Stems of billy buttons and bluebeard were considered marketable and harvested at the base of the plant once the two basal inflorescences were completely reflexed and when 1/3 of flowers were open on the singular inflorescence, respectively. At harvest, the date was recorded and time to harvest (TH) was calculated, stem length was measured from the base of the stem to the tallest point of the inflorescence, stem caliper at the thickest point of the stem was measured, and number of branches on each harvest stem was recorded. Billy buttons and bluebeard plants were monitored for 12 and 11 weeks, respectively, to record the total number of marketable flowers produced under each photoperiod.

The experiment was organized in a randomized complete block design and was repeated twice over time. Plants were blocked by photoperiod with 10 experimental units (individual

plants) of each cultivar per photoperiod treatment per replication. Data from individual reps were analyzed separately when interactions between reps were present and data were pooled when no interactions were present. Data were analyzed using SAS (version 9.4; SAS Institute, Cary, NC, United States) mixed model procedure (PROC MIXED) for analysis of variance (ANOVA), and means were separated by Tukey's honest significant difference (HSD) test at $P \le 0.05$.

Results

Time to visible inflorescence

Under all photoperiods, billy buttons 'Paintball Globe' and 'Paintball Poppy' produced Vis and flowered (Fig. 1A and 1B). As the daylength increased from 9 to 16 h, Time to visible inflorescence (TVI) decreased from 43 to 28 d for 'Paintball Globe' and from 17 to 11 d for 'Paintball Poppy' (Fig. 1A and 1B). Under a 4-h NI, TVI was 34 and 14 d for 'Paintball Globe' and 'Paintball Poppy', respectively.

Similarly, both bluebeard varieties produced Vis under all photoperiods investigated (Fig. 2A and 2B), but those inflorescences only developed when the daylength was ≤ 15 and ≤ 14 h for 'Pagoda Lagoon' and 'Pagoda Dark Pink', respectively (Fig. 2C and 2D). TVI was also influenced by photoperiod — as photoperiod increased from 9 to 16 h, 'Pagoda Lagoon' TVI increased from 19 to 47 d and 'Pagoda Dark Pink' increased from 18 to 49 d (Fig. 2A and 2B). Under a NI, TVI of both bluebeard varieties averaged »42 to 43 d.

Time to harvest

'Paintball Globe' and 'Paintball Poppy' stems were marketable under all photoperiod treatments (Fig. 1C and 1D). Generally, TH decreased from 70 to 55 d and 50 to 38 d for 'Paintball Globe' and 'Paintball Poppy', respectively, grown under photoperiods ³13 h compared to plants grown under a 9 h photoperiod.

Inflorescences of 'Pagoda Lagoon' and 'Pagoda Dark Pink' only developed into flowers and were marketable under photoperiods £15 and £14 h, respectively, during the 77 d of the study (Fig. 2C and 2D). TH of 'Pagoda Lagoon' increased from 38 to 52 d as daylength increased from 9 to 15 h. Daylength, however, did not have a large influence on TH of 'Pagoda Dark Pink'; TH increased by »3 d as daylength increased from 9 to 14 h.

Cut flower morphology at harvest

'Paintball Globe' and 'Paintball Poppy' stem length increased from 69 to 105 cm and 57 to 70 cm as the daylength increased from 9 to 16 h, respectively (Fig. 1E and 1F). Under an NI, the stem length of both varieties was similar to those under a 12-h photoperiod. Stem caliper of 'Paintball Globe' and 'Paintball Poppy' were not significantly influenced by the photoperiod, averaging »4.5 and »4.8 mm for each respective cultivar (data not presented).

Stem length of bluebeard 'Pagoda Lagoon' and 'Pagoda Dark Pink' increased as photoperiod increased from 9 to 15 h and 9 to 14 h for 'Pagoda Lagoon' and 'Pagoda Dark Pink', respectively (Fig. 2E and 2F). However, marketable stems (>40 cm) were only harvested under ³10 h for 'Pagoda Lagoon' and ³13 h for 'Pagoda Dark Pink'. At harvest, stems of 'Pagoda Lagoon' grown under 15 h averaged a stem caliper of »4.6 mm, while stems grown under a photoperiod £14 had an average stem caliper of <3.5 mm (data not presented). The number of nodes below the first open flower on 'Pagoda Lagoon' stems at harvest was also influenced by photoperiod, but no discernable trends were observed (data not presented). Stems grown under photoperiods <13 had »1 fewer node than those grown under a 14 and 15 h photoperiod. The number of nodes and stem caliper of 'Pagoda Dark Pink' stems at harvest grown under 9 to 14 h photoperiods were not significantly different. For 'Pagoda Lagoon', the number of branches per stem increased as stem length increased, in response to increasing photoperiod (data not presented). Stems grown under 15 h averaged »14 branches, which is »5 more branches than stems grown under 12-, 13-, and 14-h photoperiods and »9 more branches than stems grown under 9-, 10-, and 11-h photoperiods. For 'Pagoda Dark Pink', the number of branches per stem was »11 on stems harvested under 14 h, while the number of branches on stems grown under 9 to 13 h were not significantly different (data not presented).

During Rep. 1, 'Paintball Globe' produced 2 and 4 harvestable stems, under a 9- and 16-h photoperiod, respectively (Fig. 1G). For 'Paintball Poppy', there was no significant difference between the total number of stems harvested per plant as photoperiod increased; all treatments averaged 1 marketable stem per plant (Fig. 1H).

The total number of stems harvested per plant for 'Pagoda Lagoon' was similar for plants grown under 9 to 14-h photoperiods, averaging »5 marketable stems per plant, while plants grown under a 15-h photoperiod produced an average of 2 marketable stems per plant (Fig. 2G). For 'Pagoda Dark Pink', the total number of marketable stems harvested per plant was not significantly different, averaging »4-5 marketable stems per plant under all photoperiod treatments (Fig. 2H).

Discussion

Billy buttons 'Paintball Globe' and 'Paintball Poppy' developed inflorescences under all daylengths tested; however, TVI and TH of 'Paintball Globe' was hastened under daylengths ≥13 h. These results are consistent with other studies on photoperiodic lighting of *Pcynosorus* varieties specifically bred for cut flower production (Orvos and Lyons, 1989; Annis et al., 1992). Annis et al. (1992) reported that TVI and anthesis of billy buttons grown under a 15-h LD were

reduced by 20 and 11 d, respectively, compared to plants under an 11-h SD. Other Asteraceae species have been reported to demonstrate similar responses; for example, shasta daisy (*Chrysanthemum maximum*) 'Esther Read' remained vegetative under £12 h photoperiods, while plants reached anthesis under photoperiods ³13 h (Griffin and Carpenter, 1964). *Rudbeckia hirta* 'Marmalade' demonstrated a quadratic relationship between plant height and the number of LDs received, with plant height increasing with additional LD exposure (Orvos and Lyons, 1989).

In terms of plant productivity, the number of harvestable 'Paintball Globe' stems produced increased as photoperiod increased, while no difference was observed for 'Paintball Poppy'. Annis et al. (1992) reported that LD exposure increased the number of flowers produced; there were 0.3 under SDs and 7.5 under LDs (Annis et al., 1992).

'Paintball Globe' and 'Paintball Poppy' stem length increased as photoperiod increased from 9 to 16 h. This could be attributed to longer exposure to a low R:FR ratio emitted from the LED lamps. Stem extension is influenced by the R:FR ratio and stem lengths of LD plants such as Carpathian bellflower (*Campanula carpatica*), coreopsis (*Coreopsis grandiflora*), and pansy (*Viola* ×wittrockina) were shown to similarly increase as the R:FR ratio decreased (Runkle and Heins, 2001). Increased exposure to a low R:FR could also have influenced the accelerated flowering of billy buttons plants under photoperiods \geq 12 h. A low R:FR can lead to accelerated flowering in LDPs including Carpathian bellflower and baby's breath (*Gypsophila paniculata*) based on exposure to inductive photoperiods and light quality (i.e. low R:FR) because of its role as an environmental signal for flower induction (Kristiansen, 1988; Nishidate et al., 2012; Demotes-Mainard et al., 2016).

Many flowering perennial species are characterized as obligate or facultative LDPs and flower during the LDs of summer when the daylength exceeds 12 or 13 h (Runkle et al., 1996).
However, several perennial species that exhibit facultative SDP responses to photoperiod exist, flowering later in the season as daylength becomes shorter. In addition to bluebeard, goldenrod (Solidago \times hybrida) and aster (Symphyotrichum spp.) demonstrate a facultative SDP response for flower induction and development. Goldenrod requires SDs for flower induction, perceiving the shorter day lengths as an environmental signal to initiate flowering (Kazaz and Karagüzel, 2010). Asters produced for cut flowers exhibit a strong thermophotoperiodic response. LDs promote stem elongation; however, the exact critical photoperiod is dependent on the temperature (Lopez et al., 2006). Flower induction of aster occurs under a critical photoperiod of ≤ 10 h, while flower development and organogenesis are not influenced by photoperiod (Schwabe, 1985; Lopez et al., 2006). Although botanically these plants may be classified as facultative SDPs, classifying them as obligate SDPs for flower induction from a commercial horticultural perspective may be beneficial for cut flower growers. An understanding of the flowering physiology of herbaceous perennials is crucial for achieving a consistent flower yield (Enfield et al., 2004). Implementing this knowledge in a production environment involves using black cloth to cover plants, effectively blocking out light pollution and inducing a SD environment if the natural daylength exceeds the critical SD photoperiod or growing them when the natural daylengths are appropriate (Runkle et al., 1996).

Modern cut flower varieties of bluebeard 'Pagoda Lagoon' and 'Pagoda Dark Pink' developed inflorescences under all photoperiods tested; however, flower induction did not occur at the same time, classifying it as a facultative SDP for flower induction. For flower development, it should be classified as an obligate SDP as inflorescences only developed into open flowers under £15 h and £14 h, respectively. Therefore, the critical photoperiod for 'Pagoda Lagoon' and 'Pagoda Dark Pink' was 15 h and 14 h, respectively. These results are consistent

with Piringer et al. (1963) who reported that *Caryopteris ´clandenensis* developed flower inflorescences under an 8-, 12-, and 16-h photoperiod or a 3-h NI. However, flower development only occurred under the 8- and 12-h photoperiods. In contrast, Armitage and Son (1992) reported that flower inflorescence induction of *Caryopteris incana* only occurred on plants grown under an 8- or 12-h photoperiod, while plants under a 16-h photoperiod remained vegetative. These discrepancies in flower inflorescence induction can be attributed to the different species utilized in each study (*C. incana* versus *C. ´ clandenensis*), where *C. ´clandenensis* is a hybrid of *C. incana ´ C. mongholica* (Armitage and Son, 1992).

The flowering responses in the current study are consistent with flowering of bluebeard varieties grown outdoors under natural daylengths in USDA hardiness zones 6 through 9. Plants naturally flower from late summer into fall, providing a bright violet color during the fall season (NC State Extension, n.d.). Growing bluebeard under a photoperiod similar to the daylength during the fall season is critical for production; however, as the days become shorter, the correlation between flowering and stem length should be considered.

Between the two experimental replications, there were differences between the number of branches and the caliper of bluebeard stems (data not presented). This could be attributed to the 38% difference in DLI between the two replications (Rep. 1 DLI of 11 mol×m⁻²×d⁻¹, Rep. 2 DLI of 8 mol×m⁻²×d⁻¹). Spall and Lopez (2024) observed that producing dianthus (*Dianthus barbatus*) 'Amazon Neon Cherry' and 'Amazon Rose Magic' under a low and moderate DLI of *5 and *10 mol×m⁻²×d⁻¹, respectively, resulted in differences in branch number, caliper, and inflorescence number. Under a moderate DLI, both dianthus varieties had *7-8 fewer branches at harvest compared to those finished under a low DLI. Additionally, Cavins and Dole (2001) reported that stem caliper of campanula (*Campanula medium*) 'Champion Blue' and 'Champion

Pink' was up to 13 and 6% thicker when finished under a low DLI without supplemental lighting, compared to stems grown under a more moderate DLI with supplemental lighting providing $>90 \mu mol \times m^{-2} \times s^{-1}$ for 8 h·d⁻¹.

In conclusion, the present study suggests that billy buttons 'Paintball Globe' and 'Paintball Poppy' can be produced under any photoperiod between 9 to 16 h; however, time to harvest is hastened under photoperiods \geq 13 h for 'Paintball Globe'. Market standards indicate that cut flower stems must have a minimum length of \geq 60 cm to command a premium price; however, stem lengths averaging between 30 to 41 cm may be marketable depending on the cut flower variety (Ahmad et al., 2017; Ortiz et al., 2012; Starman et al., 1995). Stem length of 'Paintball Globe' and 'Paintball Poppy' under all photoperiods exceeded 60 cm. Bluebeard 'Pagoda Lagoon' and 'Pagoda Dark Pink' grown under a 9-h photoperiod were unmarketable because their stem lengths were \leq 30 cm as plants flowered after only 19 and 18 d, respectively, of being placed under treatments. 'Pagoda Lagoon' grown under \geq 14 h produced stems >50 cm, while 'Pagoda Dark Pink' stems did not reach 50 cm under any photoperiod.

From a horticultural standpoint, growers should provide billy buttons with daylengths \geq 12 h to hasten time to harvest, increase yield, and stem quality, and allowing for succession planting if desired. Bluebeard varieties should be grown under a 16-h photoperiod or NI for vegetative growth for 4 to 6 weeks and then provided with daylengths of 11 to 14 h to ensure a timely harvest and a marketable stem length. To ensure steady production, growers previously restricted to producing bluebeard and billy buttons outdoors or in high tunnels in temperate regions can utilize these guidelines to produce these plants year-round in greenhouses.

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Photoperiod (h)	DLI (mol×m ⁻² ×d ⁻¹)	MDT (°C)	Day (°C)	Night (°C)
		Ren 1		
9	112 + 53	213 + 31	23 1 + 2 1	196+21
10	10.5 ± 5.2	21.3 ± 3.1 20.8 ± 2.6	23.1 ± 2.1 22.0 ± 1.7	19.0 ± 2.1 19.5 ± 2.1
10	10.3 ± 5.2 10.3 ± 5.6	20.0 ± 2.0 21.0 + 2.8	22.0 ± 1.7 22.7 ± 1.9	19.3 ± 2.1 19.3 + 1.4
12	10.5 ± 3.0 11.5 ± 7.0	21.0 ± 2.0 20.5 ± 2.6	22.0 ± 1.8	19.0 ± 1.1 19.0 ± 1.6
13	10.3 ± 4.5	20.6 ± 3.1	22.5 ± 2.0	19.0 ± 1.0 19.7 ± 1.4
14	11.4 + 5.5	20.7 ± 2.7	22.3 ± 1.7	19.2 ± 1.5
16	11.2 ± 5.1	20.3 ± 3.4	22.6 ± 1.7	19.1 ± 1.8
4-h NI	11.3 ± 5.7	21.0 ± 3.6	22.6 ± 1.7	19.4 ± 1.1
		Rep. 2		
9	7.5 ± 2.9	19.8 ± 1.1	22.9 ± 1.1	16.7 ± 1.4
10	8.6 ± 2.1	19.9 ± 1.1	22.9 ± 1.2	16.9 ± 1.5
11	8.1 ± 2.2	19.6 ± 1.2	22.2 ± 1.2	17.1 ± 1.5
12	7.3 ± 3.2	21.0 ± 1.1	23.2 ± 1.2	18.9 ± 1.4
13	8.3 ± 3.0	21.1 ± 1.2	23.0 ± 1.2	19.2 ± 1.5
14	_z	20.3 ± 0.9	22.5 ± 1.1	18.2 ± 1.2
15	8.3 ± 3.3	20.1 ± 0.9	22.3 ± 1.1	17.9 ± 1.2
16	7.9 ± 2.1	20.8 ± 1.2	22.3 ± 1.4	17.4 ± 1.6
4-h NI	7.8 ± 3.2	19.3 ± 1.2	21.7 ± 1.2	16.9 ± 1.7

Table 1. Actual daily light integral (DLI) [mean \pm SD (mol \times m⁻² \times d⁻¹)], air mean daily temperature (MDT), day temperature, and night temperature [mean \pm SD (°C)] throughout the duration of the bluebeard and billy buttons finishing stages for reps. 1 and 2.

^zNo data recorded.



Figure 1. Effect of 9-, 10-, 11-, 12-, 13-, 14-, 15-, or 16-h photoperiod or a 4-h night interruption (NI) on days to visible inflorescence (A; B), days to harvest (C; D), stem length (E; F), and stems harvested per plant (G; H) of billy buttons (*Pycnosorus globosus*) 'Paintball Globe' and 'Paintball Poppy'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate the standard error of the mean. Solid circles indicate the pooled Rep. 1 and 2 mean of 20 plants. For (G), solid circles represent the mean of 10 plants in Rep.1 and open circles indicate the mean of 10 plants in Rep. 2.



Figure 2. Effect of 9-, 10-, 11-, 12-, 13-, 14-, 15-, 16-h or a 4-h night interruption (NI) on days to visible inflorescence (A; B), days to harvest (C; D), stem length (E; F), and stems harvested per plant (G; H) of Bluebeard (*Caryopteris incana*) 'Pagoda Lagoon' and 'Pagoda Dark Pink'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate the standard error of the mean. Solid circles indicate the pooled Rep. 1 and 2 mean of 20 plants.

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CHAPTER 3

Vernalization temperature and duration, and forcing daylength influence time to harvest, stem length, and yield of *Ranunculus asiaticus* specialty cut flowers Vernalization temperature and duration, and forcing daylength influence time to harvest, stem length, and yield of *Ranunculus asiaticus* specialty cut flowers

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Abstract

As the demand for locally grown specialty cut flowers increases, growers in temperate regions are interested in producing cool-season varieties to diversify and extend their sales. Ranunculus, or Persian buttercup (*Ranunculus asiaticus*), are high value cut flowers that are typically grown in the late winter to early spring because they are intolerant of high temperatures. Most ranunculus production takes place in fields and high tunnels; however, controlled environment production in greenhouses offers the opportunity for temperature and photoperiod manipulation to meet specific market dates. Our objectives were to determine how time to visible flower bud and harvest, yield, and stem quality of ranunculus 'Amandine Black', 'Butterfly Artemis', 'La Belle White', and 'Tecolote Salmon' are influenced by vernalization temperature and duration provided to rehydrated tuberous roots and by the daylength provided during greenhouse forcing. Tuberous roots were rehydrated for 8 h in aerated water and subsequently planted into trays and placed in a growth chamber for 4 weeks of pre-sprouting at 5.5 °C and under a 12-h photoperiod. In Expt. 1, trays were placed in vernalization treatments for 0, 2, or 3 weeks at 3.5, 5.0, or 7.5 °C and 0, 2, or 3 weeks at 3.5 and 7.5 °C in Expt. 2. Sprouted plants were transplanted into bulb crates and moved to a greenhouse with an average daily temperature of 13 °C and a 12-, 14-, or 16-h photoperiod for 8 weeks. In Expt. 2, plants were forced under a 12-h photoperiod for five weeks to promote vegetative growth before being moved to a 12-, 14-, or 16-h photoperiod. Time to visible bud was influenced by vernalization temperature and duration for 'Amandine Black', 'Butterfly Artemis', and 'La Belle White'. Time to visible bud of 'Amandine Black', 'Butterfly Artemis', and 'La Belle White' was accelerated by at least 8 d when tuberous roots were vernalized at 3.5 °C for at least 2 weeks. Time to harvest was influenced by vernalization temperature and duration and finishing photoperiod for

'Amandine Black' and 'La Belle White', while time to harvest for 'Butterfly Artemis' was influenced by only vernalization duration and finishing photoperiod. Time to harvest of 'Amandine Black' and 'La Belle White' was accelerated by at least 9 d when tuberous roots were vernalized at 3.5 °C for at least 2 weeks and finished under 16-h photoperiod, while time to harvest of 'Butterfly Artemis' was accelerated by at least 9 d when tuberous roots were vernalized for at least 2 weeks and finished under a 16-h photoperiod, regardless of vernalization temperature. Stem length was greatest under the 12-h photoperiod, while plants grown under the 16-h photoperiod were shortest. Based on these results, vernalizing hydrated tuberous roots for 2 weeks at 3.5 to 7.5 °C can reduce time to harvest of ranunculus stems. Forcing under daylengths ≥14 h also reduced time to harvest, but plants grown under 12 h had the longest stems.

Keywords: Persian buttercup, flower induction and development, cold treatment, photoperiodic lighting

Abbreviations: DLI, daily light integral; LD, long day; LED, light-emitting diode; MDT, mean daily temperature; PPFD, photosynthetic photon flux density; SD, short day; TTH, time to harvest; TVB, time to visible bud; VB, visible flower bud

Introduction

A large percentage of cut flowers purchased in the United States are imported from Colombia, Ecuador, and the Netherlands, with only 20% of wholesale flowers produced domestically in 2013 (Li et al., 2016; Faust and Dole, 2021; Rauter et al., 2022). In recent years, there has been an increased consumer demand for new, diverse, and domestically grown specialty cut flowers (Darras, 2021). In response to this demand, small-scale domestic markets cultivating niche, seasonal, high-value cuts have developed. This domestic market can compete with international markets by growing high-value species that are not typically imported due to their shorter vase life (Wien and Pritts, 2008; Yue and Hall, 2010). Specialty cuts are generally grown in smaller quantities for sale to local florists or direct to consumer markets such as farmer's markets, and you-pick or roadside stands (Armitage, 1993; Darras, 2021). Specialty cut flowers are commonly grown seasonally in fields and high tunnels due to economic feasibility with limited season extension in northern latitudes (Ortiz et al., 2012). Consequently, there has been increased interest in controlled-environment greenhouse production in temperate climates to enable year-round local and regional markets. This production system allows growers to manipulate environmental parameters to provide inductive growing conditions and schedule flowering to meet specific market dates year-round (Hasna et al., 2024).

Ranunculus (*Ranunculus asiaticus*) (family Ranunculaceae), commonly known as Persian buttercup, is a cool season flowering perennial geophyte that is commercially produced as a potted plant and cut flower (Fusco et al., 2023). Valued for its tight flower buds, cup-shaped flowers resembling peonies, and thin petals, ranunculus is an aesthetically popular cut flower (Missouri Botanical Garden, n.d.). However, its availability when produced domestically is generally limited to the spring because it is intolerant of extreme heat or cold. It is a

commercially important cut flower produced mainly in California, France, Israel, Italy, Japan, the Netherlands, and South Africa (De Hertogh, 1996). In 2021, the Netherlands and Italy produced 271 and 55 million stems valued at \$61 and \$30 million USD, respectively (International Statistics Flowers and Plants, 2021). The wholesale value of ranunculus stems can range from \$28 to \$172 USD per m², regardless of the production system utilized (Rauter et al., 2022). Due to the seasonality of harvests and large variability in price per stem and yield, it is desirable to identify production practices that can lead to rapid, uniform, and complete flower induction year-round.

Ranunculus are known as resurrection geophytes because their claw-like tuberous roots, rhizomes, or corms, can tolerate long quiescence or prolonged storage (Beruto et al., 2009). From seed and micropropagation, the tuberous roots are harvested, dried and graded as small (2 to 3 cm) and large (5 to 7 cm) rhizomes (Beruto et al., 2019). It is endemic to eastern Mediterranean regions where winters are characteristically cool and wet, and summers are hot and dry (Armitage, 1993). During the summer months, leaves senesce, and plants go into dormancy. A cold period accompanied by rain is necessary for the tuberous roots to break dormancy and rehydrate. Vegetative development in the form of rosette leaves occurs during the cool winter months (Beruto et al., 2018). Floral induction occurs when six to eight leaves have formed, flowering from late winter through spring (Horovitz, 1985; White, 2002).

Many geophyte crops require a period of low temperatures to accelerate flowering, and commercial production practices incorporate a cooling period to hasten flowering to meet market dates. The duration of low-temperature exposure is crucial for flower development. The absence of this cooling period can result in flowering delays or disorders and slow shoot growth (Kamenetsky and Okubu, 2012). Generally, a low temperature (i.e above 0 °C and below 7 °C) is

crucial for the development of a flower stalk and well-formed flowers (De Hertogh and Le Nard, 1993). For example, Easter (*Lilium longiflorum*) and Asiatic lilies (*Lilium auratum*) are economically important ornamental crops that require exposure to cold temperatures at the beginning of production to ensure flower initiation and development.

As a spring geophyte, ranunculus is exposed to a period of cool temperatures (i.e. vernalization) in its native environment, where a complete lifecycle consists of a warm-cold-warm sequence for growth and development (De Hertogh and Le Nard, 1993). Cold treatments improve ranunculus flowering by both shortening time to flower and increasing total flowers per plant (Beruto et al., 2009). However, published information regarding pre-sprouting and vernalization of ranunculus tuberous roots is often inconsistent or contradictory; it is indicated that pre-sprouting is the initial treatment after tuberous root rehydration to establish roots and leaves, and vernalization is the cold treatment given to established plants to mimic the cool, wet winters of their endemic, Mediterranean environment and an external cue for flowering (Kamenetsky et al., 2005; Beruto et al., 2018). Rauter and Stock (2023) reported that tuberous roots pre-sprouted in trays for at least 2 weeks at 1.5 to 10 °C can be harvested up to 1 week sooner than those directly planted, alongside increased yield for field and high tunnel planting. Armitage (1993) recommended pre-sprouting rehydrated tuberous roots at 1 to 2 °C for 2 weeks to accelerate production of the first three flowers.

Regarding vernalization, Ozeri et al. (1990) suggested soaking dry tuberous roots for 12 to 18 h followed by 3 weeks at 5 to 6 °C. Meynet (1993) recommended fully hydrating tuberous roots to full turgor to achieve uniform growth. Other studies have reported that rehydrated tuberous roots should be vernalized at 8 to 10 °C for 5 weeks under a photosynthetic photon flux density (PPFD) of 40 to 50 μ mol·m⁻²·s⁻¹ for 8 h·d⁻¹ until emergence (Buerto et al., 2009), at 10

°C for 4 weeks (Margherita et al, 1996), while Ohkawa (1986) recommends a cold treatment at 5 °C for 4 weeks. Other sources recommended cooling periods of 2 to 4 weeks or 4 to 5 weeks at 2 to 5 °C or 4 to 10 °C, respectively, to advance harvest (De Hertogh, 1996; Dole, 2003; Rauter et al., 2022).

Additionally, flower induction of ranunculus is accelerated by long days (LD) (Ohkawa, 1986; Karlsson, 1996). Yield, however, was reported to be lower under LDs compared to plants grown under short days (SD) or natural daylengths in the spring. Similarly, safflower (*Carmanthus tinctorius* L.) 'Lasting Yellow' cut flowers are classified as facultative LD plants but should be grown under 8- or 12-h photoperiods before providing inductive LDs to achieve the highest yield (Dole, 2015).

Although there are established production techniques for spring-grown field and high tunnel ranunculus, inconsistent vernalization and forcing information make it challenging for year-round production in greenhouses. Therefore, the objectives of this study were to determine how time to visible bud and harvest, yield, and stem quality of greenhouse grown ranunculus are influenced by 1) the vernalization temperature and duration provided to rehydrated tuberous roots and 2) the photoperiod during forcing.

Materials and Methods

On 11 Nov. 2023 (Expt. 1) and 19 Oct. 2023 (Expt. 2), 2- to 3-cm tuberous roots of ranunculus 'Tecolote Salmon' (Expt. 1 only), 'Amandine Black' (Expt. 2 only) and 'La Belle White' and 5- to 7-cm tuberous roots of 'Butterfly Artemis' were received from a commercial distributor where they were stored for ≈6 weeks at 18 °C (Ednie Flower Bulb, Newton, NJ). They were placed in mesh bags and submerged into aerated 20 °C water for rehydration. After 8 h, they were removed from the water and planted into trays. Depending on their size, tuberous

roots were pre-sprouted in either 18- or 72- cell trays (East Jordan Plastics model AL2401-STD-BLK or model PTT72CLCV-STD-BLK) filled with 50:50 (v/v) commercial soilless medium composed of 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products Inc., Galesburg, MI) and 50% coarse perlite.

Sprouting and vernalization environment

To promote root growth and shoot development, trays were placed in a walk-in growth chamber with a constant temperature setpoint of 5.5 °C for 4 weeks of pre-sprouting. Lightemitting diodes (LED) (Ray66 Indoor PhysioSpec; Fluence Bioengineering, Austin, TX, USA) provided a PPFD of 200 μ mol·m⁻²·s⁻¹ for 12 h·d⁻¹ to provide a daily light integral (DLI) of 8.6 mol·m⁻²·d⁻¹ [as measured with a quantum sensor (Apogee SQ-500; Apogee Instruments)]. Plants were irrigated with acidified well water as needed with MSU Orchid Special [13N–1.3P–12.5K water-soluble fertilizer containing (mg·L⁻¹): 125 nitrogen, 13 phosphorus, 121 potassium, 76 calcium, 19 magnesium, 1.7 iron, 0.4 copper and zinc, 0.9 manganese, 0.2 boron, and 0.2 molybdenum (GreenCare Fertilizers Inc., Kankakee, IL)].

After four weeks, trays were randomly and equally distributed into growth chambers with a constant temperature set point of 3.5, 5.0, or 7.5 °C for 0, 2, or 3 weeks, respectively, (Expt. 1) and a constant temperature set point of 3.5 or 7.5 °C for 0, 2, or 3 weeks, respectively, of vernalization under the previously mentioned LEDs and daylength (Expt. 2).

Vegetative growth and forcing treatment environment

All trays were removed from vernalization treatments on 30 Dec. 2022 (Expt. 1) and on 07 Dec. 2023 (Expt. 2). Sprouted tuberous roots were transplanted into bulb crates (39.3 cm wide \times 59.7 cm long \times 17.8 cm tall; 0.23 m²) filled with the above-mentioned substrate (Suremix; Michigan Grower Products Inc.) and spaced with 33-cm centers at a density of 26 plants per m² (Expt.1) or spaced with 20-cm centers at a density of 43 plants per m² (Expt. 2). Crates were placed in glass-glazed greenhouse compartments in the Plant Science Research Greenhouses at Michigan State University (East Lansing, MI; lat. 43° N) with an MDT setpoint of 13 °C [(12 h/12 h) day/night 18/8 °C].

In Expt. 1, the crates were placed under a 12-, 14-, or 16-h photoperiod created with supplemental lighting from high-intensity LED fixtures (Philips GreenPower LED TopLighting; Philips, Eindhoven, Netherlands) that delivered a PPFD of $102.0 \pm 7.2 \,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [as measured with a quantum sensor (LI-250A light meter; LI-COR Biosciences)] at plant height when the outdoor light intensity was below \approx 440 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The 100-nm waveband ratios (%) emitted by the LED fixtures, defined by their blue (B; 400–500 nm), green (G; 500–600 nm), and red (R; 600–700 nm) photon flux densities (*PFD*), were 10:5:85. In Expt. 2, crates were placed under a 12-h photoperiod for 5 weeks to promote vegetative growth. On 10 Jan. 2023, the crates were placed under a 12-, 14-, or 16-h photoperiod created with the above-mentioned LED fixtures. Plants were irrigated with MSU Orchid RO Special [13N–3P–15K water-soluble fertilizer (mg·L⁻¹) 125 nitrogen, 13 phosphorus, 121 potassium, 76 calcium, 19 magnesium, 1.7 iron, 0.4 copper and zinc, 0.9 manganese, 0.2 boron, and 0.2 molybdenum; (GreenCare Fertilizers Inc.)] blended with reverse-osmosis water.

An environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada) operated exhaust fans, ridge vents, steam heating, and supplemental lighting. On each bench, a quantum sensor (Apogee SQ-500; Apogee Instruments) positioned at plant height measured PPFD every 30 s and a datalogger (CR1000X; Campbell Scientific, Logan, UT) recorded hourly averages. An aspirated thermocouple [20-gauge (.095 x .151-mm) type E, Omega Engineering, Stamford, CT] positioned in the middle of each bench

measured the air temperature at plant height every 30 s, and the datalogger recorded hourly means. The actual DLIs, MDT, and day and night temperatures during the two experiments were calculated and are provided in Table 1.

Data collection and analysis

Plants were monitored daily for the presence of the first visible flower bud (VB) and the date was recorded. The VBs were monitored until the first open flower, the date was recorded, and the stem was harvested with consideration of ranunculus marketability standards. Stems were harvested once sepals and outer petals began to open. On the date of harvest, stem length was measured from the base of the stem to the tallest point of the inflorescence and stem caliper at the thickest point of the stem was measured. The plants were monitored for the remainder of the study to determine the total number of stems each plant produced under their respective treatment.

Both experiments were organized in a randomized complete block design and repeated twice. Plants were blocked by photoperiod with 10 experimental units (individual plants) of each cultivar per vernalization temperature, duration and photoperiod treatment per replication. Data were analyzed using SAS (version 9.4; SAS Institute, Cary, NC, United States) mixed model procedure (PROC MIXED) for analysis of variance (ANOVA), and means were separated by Tukey's honest significant difference (HSD) test at $P \le 0.05$.

Results

Expt. 1 Time to visible bud

Individually vernalization temperature and duration and some interactions influenced time to visible bud (TVB) of 'Butterfly Artemis', vernalization duration and photoperiod and one interaction influenced TVB of 'La Belle White' and vernalization temperature, duration and

photoperiod individually influenced TVB of 'Tecolote Salmon' (Fig. 1, 2, and 3A, Table 2). TVB of 'Butterfly Artemis' was accelerated by 9, 9, or 8 d after sprouted tuberous roots were vernalized at 3.5, 5.0, or 7.5 °C, respectively, regardless of forcing photoperiod, compared to non-vernalized plants (Fig. 1A, Table 2). Regardless of vernalization temperature, TVB of 'La Belle White' vernalized for 2 or 3 weeks was hastened by 4 and 7 d, respectively, compared to non-vernalized plants (Fig. 2A, Table 2). Regardless of vernalization temperature and duration, TVB of vernalized 'Tecolote Salmon' forced under a 12-, 14-, or 16-h photoperiod was hastened by 5, 6, or 6 d, respectively, compared to non-vernalized plants (Fig. 3A, Table 2).

Expt. 1 Time to harvest

Individually, vernalization temperature and duration, and forcing photoperiod influenced time to harvest (TTH) of 'Butterfly Artemis' and vernalization duration and photoperiod influenced TTH of 'La Belle White' and 'Tecolote Salmon' (Table 2). Regardless of vernalization temperature, TTH of both 'Butterfly Artemis' and 'Tecolote Salmon' was accelerated by 7 or 12 d after tuberous roots were vernalized for 2 or 3 weeks, respectively, compared to non-vernalized tuberous roots (Fig. 1 and 3B, Table 2). Similarly, TTH of 'La Belle White' was accelerated by 7 or 13 d after tuberous roots were vernalized for 2 or 3 weeks, respectively, compared to non-vernalized plants (Fig. 2B, Table 2). For 'Butterfly Artemis', 'La Belle White', and 'Tecolote Salmon' TTH was delayed by 4 or 9 d, 7 or 6 d, and 7 or 10 d when plants were forced under a 12-h or 14-h photoperiod, compared to plants under a 16-h photoperiod (Fig 1, 2 and 3B).

Expt. 1 Stem length

Stem length of 'Butterfly Artemis' was individually influenced by vernalization temperature and forcing photoperiod and some interactions, while stem length of 'La Belle White' was individually influenced by vernalization temperature and duration, and forcing photoperiod and no variable influenced the stem length of 'Tecolote Salmon' (Fig 1, 2, and 3C, Table 2). When not vernalized and forced under a 12- and 14-h photoperiod, stems of 'Butterfly Artemis' were 12 and 6 cm longer than those vernalized at 3.5 °C and forced under a 16-h photoperiod, respectively (Fig. 1C, Table 2). Harvestable stems of 'La Belle White' were 4 or 9 cm shorter after tuberous roots were vernalized for 2 or 3 weeks, respectively, compared to the stems from non-vernalized plants (Fig. 2C).

Expt. 1 Total stems harvested

The total number of stems harvested from 'Butterfly Artemis' and 'Tecolote Salmon' plants was influenced by forcing photoperiod, regardless of vernalization conditions (Fig. 1 and 3D, Table 2). The total number of stems harvested from 'La Belle White' was individually influenced by vernalization temperature and duration and forcing photoperiod, and some interactions (Fig. 2D, Table 2). When forced under a 12-h photoperiod, 'Butterfly Artemis' plants produced 5 harvestable stems, compared to 2 harvestable stems when forced under either a 14- or 16-h photoperiod (Fig. 1D). 'La Belle White' non-vernalized plants forced under a 12-h photoperiod produced 7 harvestable stems, while tuberous roots vernalized at 3.5 °C and forced under a 12-h photoperiod produced 5 harvestable stem per plant (Fig 2D).

Expt. 1 Cut flower morphology

For 'Butterfly Artemis', the number of lateral branches was independently influenced by vernalization duration and forcing photoperiod. While vernalization temperature and duration, and photoperiod did not have an influence on the number of lateral branches or diameter of stems for 'Tecolote Salmon', as well as the number of lateral branches for 'La Belle White'. However, vernalization temperature and duration independently influenced the stem diameter of 'La Belle

White' and stem diameter of 'Butterfly Artemis' was influenced by photoperiod (Table 2). Stem caliper of 'Butterfly Artemis' under a 12-, 14-, or 16-h photoperiod was 4.6, 3.5, or 3.7 mm, respectively (data not presented). Stem caliper of non-vernalized 'La Belle White' was 5 mm, while stem caliper of tuberous roots vernalized for 2 or 3 weeks was 4 or 4 mm, respectively (data not presented).

Expt. 2 Time to visible bud

Individually, vernalization temperature and duration influenced TVB of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black' (Figs. 4, 5, and 6A, Table 3). For all 3 cultivars, TVB was hastened when plants received 2 or 3 weeks of vernalizations at 3.5 or 7.5 °C regardless of the forcing photoperiod (Figs. 4, 5, and 6A). For example, TVB of 'Butterfly Artemis' and 'La Belle White' was hastened by 10 or 12 d and 10 or 11 d when tuberous roots were vernalized at a temperature of 3.5 or 7.5 °C, respectively, compared to non-vernalized plants (Figs. 4 and 5A, Table 3). TVB of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black' that received 2 or 3 weeks of vernalization was accelerated by 8 or 13 d, 8 or 14 d, and 8 or 11 d compared to non-vernalized plants (Figs 4, 5, and 6).

Expt. 2 Time to harvest

Individually, vernalization temperature and duration and photoperiod influenced TTH of 'La Belle White', and 'Amandine Black', while vernalization duration and photoperiod individually influenced TTH of 'Butterfly Artemis' (Figs. 4, 5, and 6B, Table 3). For both 'Butterfly Artemis' and 'La Belle White', TTH was accelerated by 9 or 14 d when tuberous roots were vernalized for 2 or 3 weeks, respectively, compared to non-vernalized plants (Figs. 4 and 5B, Table 3). However, regardless of vernalization temperature and duration, TTH of vernalized 'Butterfly Artemis' and 'La Belle White' forced under a 12-, 14-, or 16-h photoperiod was

hastened by 11, 13, or 10 d and 10, 12, or 12 d, respectively, compared to non-vernalized plants (Figs. 4 and 5B, Table 3). For 'La Belle White' and 'Amandine Black', TTH occurred 3 and 4 d faster, respectively, when vernalized at 7.5 °C, compared to 3.5 °C (Figs. 5 and 6B). *Expt. 2 Stem length*

Stem length of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black' was influenced independently by vernalization duration and the photoperiod during greenhouse forcing (Figs. 4, 5, and 6C, Table 3). Regardless of vernalization temperature or duration, stems of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black' under a 12, 14, or 16-h photoperiod were 37, 35, or 31 cm, 45, 44, or 38 cm, and 35, 32, or 30 cm, respectively (Figs. 4, 5, and 6C, Table 3). While stem of 'La Belle White' and 'Amandine Black' vernalized for 3 weeks were 3 or 4 cm and 4 or 4 cm shorter than plants not receiving vernalization or those receiving 2 weeks of vernalization, respectively (Figs. 5 and 6C, Table 3).

Expt. 2 Total stems harvested

Individually, vernalization duration and finishing photoperiod, vernalization temperature, and finishing photoperiod influenced the total number of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black' stems harvested per plant, respectively (Figs. 4, 5, and 6D, Table 3). For example, the number of stems harvested from 'Butterfly Artemis' forced under a 12-, 14-, or 16- h photoperiod were 3, 2, or 2 stems, respectively (Figs. 4D). 'Amandine Black' plants vernalized for 2 or 3 weeks produced 3 or 3 stems, respectively, while non-vernalized plants produced 2 stems per plant (Fig. 6D).

Expt. 2. Cut flower morphology

Vernalization temperature and duration nor forcing photoperiod had an influence on the number of lateral branches 'Butterfly Artemis' produced; however, vernalization temperature independently influenced the number of lateral branches on 'Amandine Black' stems and vernalization temperature and photoperiod independently influenced the number of lateral branches on 'La Belle White' stems (Table 3). For 'Amandine Black', the number of lateral branches on plants vernalized at a temperature of 3.5 or 7.5 °C was 0 or 1, respectively. Non-vernalized 'Amandine Black' stems had an average of 0 lateral branches (data not presented). Similarly, vernalization temperature and duration and forcing photoperiod did not independently have an influence on the diameter of 'Butterfly Artemis' stems (Table 3). Vernalization duration and temperature independently influenced the diameter of 'La Belle White' stems and vernalization duration influenced the diameter of 3.5 or 7.5 °C produced stems with a diameter of 4.0 or 4.2 mm, respectively, while non-vernalized plants produced stems with a diameter of 4.6 mm (data not presented).

Discussion

In its native environment, ranunculus is exposed to a warm-cold-warm sequence that is necessary to break dormancy in the spring. The importance of providing vernalization has been extensively reported in the literature (Ohkawa, 1986; De Hertogh, 1996; Margherita et al., 1996; Ozeri et al., 1990; Dole, 2003; Buerto et al., 2009), alongside a few studies suggesting the benefits of a pre-sprouting period prior to vernalization (Armitage, 1993; Rauter and Stock, 2023). In most instances, these studies state that flower bud initiation and development of vernalized ranunculus was hastened compared to non-vernalized plants. Other studies suggest that vernalization of tuberous roots is a precursor to sprouting, leaf formation, and flowering (Beruto et al., 2009). The results of the current study generally indicate that 2 to 3 weeks of vernalization and vernalization temperatures of 3.5 to 7.5 °C generally accelerate TVB and TTH

of 'Butterfly Artemis', 'La Belle White', and 'Amandine Black'. Additionally, the photoperiod plants are forced under needs to be carefully manipulated as it influences TVB and TTH and cut flower yield and quality.

It must be noted that subjecting ranunculus to pre-sprouting and vernalization will increase total production time. Therefore, growers can opt to vernalize sprouted ranunculus, ultimately adding 2 to 3 weeks to production timing, but not subjecting plants to vernalization may delay TTH by \approx 4 to 18 d, contingent upon the finishing photoperiod, tuber size, and cultivar (Carillo et al., 2021). Vernalization, however, does not necessarily have to take place in the greenhouse. Given that greenhouse space is often limited, vernalization can occur in coolers or hoophouses when temperatures can be controlled.

Our results are consistent with other studies investigating the influence of vernalization on flowering of geophytes, such as lilies for cut flower and potted plant production (Dole and Wilkins, 1994; Lee et al., 1996; Lee et al., 2010). Lee et al. (1996) reported that flowering of Asiatic hybrid lilies (*Lilium spp.*) was accelerated when bulbs received a minimum of 4 weeks of vernalization at 5 °C. For example, late-flowering line A Asiatic hybrid lily bulbs that received 0 or 2 weeks of vernalization flowered 247 and 234 d after planting, while bulbs that received 4, 6, 8, or 10 weeks of vernalization flowered 157, 135, 130, 127, and 193 d after planting, respectively (Lee et al., 1996). In the present study, TVB and TTH of 'Butterfly Artemis' occurred ≈9 to 12 and ≈9 to 14 d sooner than those not vernalized, regardless of vernalization temperature. These results align with Ohkawa (1986), who reported that irrespective of the planting date, ranunculus 'Hamanomeigetsu' tuberous roots that received 2 and 4 weeks of vernalization sprouted ≈50 d sooner than those not vernalized. In a separate study, Lee at al. (2010) investigated the influence of vernalization duration on flowering of Asiatic hybrid lilies (*Lilium* ×*elegans*) 'Red Carpet' and 'Sunray', subjecting bulbs to vernalization at 2.5 °C for 0, 2, 4, or 6 weeks. Flowering of non-vernalized 'Red Carpet' bulbs occurred in 100 d, while flowering was hastened by 34 and 40 d when bulbs received 4 and 6 weeks of vernalization, respectively. Furthermore, non-vernalized bulbs averaged 2.6 flowers per plant while bulbs vernalized for 6 weeks produced 6.7 flowers (Lee et al., 2010). These results do not align with our findings, as there was not a significant difference between the number of stems harvested for non-vernalized plants.

However, we reported that TTH was hastened under LD conditions (16-h photoperiod), but fewer stems were harvested from each plant compared to those grown under SD conditions (12-h photoperiod). Similar findings were reported by Ohkawa (1986); ranunculus that received a cold treatment and were forced under a 20-h photoperiod reached anthesis 40 and 46 d earlier than those under an 8-h SD and natural daylength treatments, respectively. Similar trends were observed for plants that did not receive vernalization, with total stem number being lowest under LD conditions.

Consistent with our findings, Karlsson (1996) reported that potted ranunculus 'Bloomingdale Mix' forced under an 8, 12, or 16-h photoperiod and temperatures of 12, 16, or 20 °C showed the fastest appearance of VB and time to anthesis under a 16-hour photoperiod at 16 °C, and under a 12-hour photoperiod at 20 °C. Under these conditions, the number of days to flower was approximately 53 d from the start of treatments; in contrast, plants grown under an 8h photoperiod at 16 °C and 12-h photoperiod at 12 °C were delayed by 21 d (Karlsson, 1996). These findings reiterate that LD conditions and cooler forcing temperatures accelerate flowering, as ranunculus plants do not tolerate high temperatures and often cease flower production when the average daily temperature consistently exceeds 25 °C (Rauter et al., 2022). Flower

production was also accelerated under a non-inductive photoperiod combined with a warmer, tolerated temperature of 20 °C (Karlsson, 1996). As previously mentioned, ranunculus is sensitive to photo-thermoperiodism, exhibiting a facultative LD response when temperatures are below 25 °C. Other crops showing similar responses include *Rudbeckia spp.*, considered a facultative LD regardless of vernalization (Kochankov and Chailakhyan, 1985; Runkle et al., 1999). However, up to 15 weeks of vernalization at 5 °C hastened flowering of *Rudbeckia* 'Goldsturm' by up to 4 weeks, demonstrating a sensitivity to photo-thermoperiodism (Nau, 1996; Runkle et al., 1999).

In Expt. 1, plants were placed under forcing photoperiods of 12-, 14-, or 16-h directly after vernalization. In Expt. 2, plants were grown under a 12-h photoperiod for 5 weeks after vernalization to promote vegetative growth, before being placed under the forcing photoperiods. During Expt. 2, TVB and TTH was hastened by ≈20 to 30 d compared to Expt. 1. For example, TVB and TTH of 'La Belle White' vernalized for 2 weeks at 3.5 °C and finished under a 12-, 14-, and 16-h photoperiod during Expt. 2 was accelerated by 22, 28, and 23 d and 30, 33, and 27 d, respectively, compared to plants in Expt. 1. In Expt. 2, vegetative growth was promoted by placing plants under a 12-h SD for 5 weeks prior to forcing under LDs; this consequently hastened TVB and flower development.

In Expt. 1, generally TTH of 'Tecolote Salmon' was most notably reduced when plants were vernalized for 3 weeks at 7.5 °C and subsequently grown under inductive LDs of 16 h. TTH was delayed for non-vernalized plants that were finished under a 16-h photoperiod, indicating LD conditions do not effectively substitute for vernalization in regard to accelerated flowering. In a greenhouse experiment, Dole and Wilkins (1994) investigated the interaction between bulb vernalization and photoperiod during forcing of 'Nellie White' Easter lily (*Lilium*

longiflorum) to determine if LDs could effectively replace a cold treatment. Providing LDs after shoot emergence did not equally substitute for a cold treatment — shortening the cold treatment duration delayed TVB. For Easter lily production, using LD in combination with a cold treatment could allow growers to reduce time in the cooler; however, due to there being a reported increase in days from emergence to visible bud with decreasing weeks of cold treatment, more time in the greenhouse would be required.

In Expt. 1 and 2, the environmental variables influencing TTH and stem length of 'Butterfly Artemis' were consistently different than those influencing 'Amandine Black', 'La Belle White', or 'Tecolote Salmon'. These discrepancies could be attributed to the hybridization of ranunculus varieties. Commercial ranunculus breeders aim to improve flower diameter, morphology, and color; however, hybridization can lead to changes in physiological processes such as early flowering and branching (Buerto et al., 2018). The Amandine and La Belle series demonstrate many similarities compared to the Butterfly series. This series has been bred to produce multiple flowers per stem and rhizomes are generated from tissue culture (Ball Seed, 2023).

In conclusion, the results of Expt. 1 and 2 indicate that vernalizing pre-sprouted ranunculus tuberous roots for 2 to 3 weeks at vernalization temperature of 3.5 to 7.5 °C accelerated TVB and TTH from the beginning of the forcing period compared to plants that did not receive vernalization. The interaction between vernalization and finishing photoperiod can further hasten TTH; in some cases, flowering occurred earlier under LDs. Our results indicate that TTH is further hastened when plants are grown under SDs for 4 to 5 weeks prior to forcing under LDs. Choosing not to provide vernalization will delay flowering under inductive daylengths, but depending on the cultivar, flowering may be delayed by 4 to 18 d. However,

vernalization may not decrease overall production time when the number of weeks of vernalization is considered and should be accounted for when scheduling crops. Stem length of ranunculus is primarily influenced by the finishing photoperiod, and while a 16-h photoperiod can hasten flowering, the stems produced were fewer and shorter than those produced under a 12 h photoperiod. However, stem lengths were between 30 to 41 cm and are considered marketable (Starman et al., 1995; Ortiz et al., 2012), and stems produced under all photoperiods tested were considered marketable.

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Photoperiod (h)	DLI	MDT (°C)	Day (°C)	Night (°C)
	$(\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1})$			
		Expt. 1		
12	13.5 ± 6.4	12.9 ± 5.6	17.0 ± 0.9	8.7 ± 1.4
12	13.6 ± 5.7	13.0 ± 5.4	17.1 ± 0.8	9.0 ± 1.6
14	14.1 ± 6.2	13.1 ± 5.6	17.3 ± 0.8	8.9 ± 1.5
14	13.7 ± 4.5	13.1 ± 5.5	17.1 ± 1.0	9.1 ± 1.4
16	14.6 ± 5.5	12.7 ± 5.8	16.8 ± 1.2	8.6 ± 1.3
16	13.3 ± 5.9	13.1 ± 5.4	17.1 ± 1.2	9.1 ± 1.4
		Expt. 2		
12	12.6 ± 3.5	13.3 ± 1.2	18.4 ± 1.0	8.4 ± 1.9
12	12.8 ± 2.6	13.3 ± 1.0	18.4 ± 0.7	8.2 ± 1.7
14	12.9 ± 2.7	13.5 ± 1.3	18.5 ± 1.1	8.5 ± 1.9
14	12.0 ± 2.8	14.0 ± 1.9	18.7 ± 1.7	9.3 ± 2.6
16	13.3 ± 3.7	13.7 ± 1.3	19.0 ± 1.2	8.5 ± 1.8
16	12.5 ± 2.8	13.4 ± 1.1	18.3 ± 0.8	8.5 ± 1.8

Table 1. Actual daily light integral (DLI) (mean \pm SD), air mean daily temperature (MDT), and day and night temperature (mean \pm SD) throughout the duration of the ranunculus finishing stages for Experiments 1 and 2.

						Total stems
	Days to visible	Days to harvest	Stem length	Stem caliper	Branches	harvested per
	bud (no.)	(no.)	(cm)	(mm)	(no.)	plant (no.)
	Butterfly Artemis					
Dur	*	***	NS	NS	**	NS
Temp	*	**	*	NS	NS	NS
Photo	NS	***	***	***	**	***
Dur × temp	*	NS	NS	NS	NS	NS
$Dur \times photo$	*	NS	*	*	NS	NS
Temp × photo	*	NS	***	NS	NS	NS
$Dur \times temp \times photo$	NS	NS	*	NS	NS	NS
1 1	La Belle White					
Dur	***	***	***	***	NS	***
Temp	**	NS	***	*	NS	**
Photo	***	***	***	NS	NS	***
Dur × temp	NS	NS	NS	*	NS	NS
Dur × photo	NS	NS	NS	NS	NS	NS
Temp \times photo	*	NS	***	*	*	***
$Dur \times temp \times photo$	NS	NS	NS	NS	NS	NS
	Tecolote Salmon					
Dur	***	***	NS	NS	NS	NS
Temp	NS	NS	NS	*	NS	NS
Photo	***	***	NS	NS	NS	*
Dur × temp	NS	NS	NS	NS	NS	NS
Dur × photo	NS	NS	NS	NS	NS	NS
Temp \times photo	NS	NS	NS	NS	NS	NS
$Dur \times temp \times photo$	NS	NS	NS	NS	NS	NS

Table 2. Analyses of variance for the effects of vernalization duration and temperature, and finishing photoperiod, and their interaction on time to visible bud, time to harvest, stem length and caliper, branches, and total stems harvested per plant during Experiment 1.

NS, *, **, *** Nonsignificant or significant at $P \le 0.05$, 0.01, and 0.001, respectively.

						Total stems
	Days to visible bud	Days to harvest	Stem length	Stem caliper	Branches	harvested per
	(no.)	(no.)	(cm)	(mm)	(no.)	plant (no.)
	Butterfly Artemis					
Dur	***	***	*	NS	NS	*
Temp	**	NS	NS	NS	NS	NS
Photo	NS	**	***	NS	NS	***
Dur × temp	NS	NS	NS	NS	NS	NS
$Dur \times photo$	NS	NS	NS	**	NS	NS
Temp \times photo	NS	NS	NS	NS	**	NS
$Dur \times temp \times photo$	NS	NS	NS	NS	NS	NS
	La Belle White					
Dur	***	***	***	*	NS	NS
Temp	***	***	NS	**	***	**
Photo	*	***	***	NS	**	NS
$Dur \times temp$	NS	NS	NS	NS	NS	NS
$Dur \times photo$	NS	NS	NS	*	NS	NS
Temp \times photo	*	**	*	NS	NS	NS
$Dur \times temp \times photo$	NS	NS	NS	NS	NS	NS
1 1	Amandine Black					
Dur	***	***	***	**	NS	***
Temp	***	***	NS	NS	***	NS
Photo	NS	*	***	NS	NS	NS
$Dur \times temp$	NS	NS	NS	NS	NS	NS
$Dur \times photo$	*	**	NS	NS	NS	*
Temp × photo	*	NS	NS	NS	*	NS
$Dur \times temp \times photo$	NS	NS	NS	NS	NS	NS

Table 3. Analyses of variance for the effects of vernalization duration and temperature, and finishing photoperiod, and their interaction on time to visible bud, time to harvest, stem length and caliper, branches, and total stems harvested per plant during Experiment 2.

NS, *, **, *** Nonsignificant or significant at $P \le 0.05$, 0.01, and 0.001, respectively.



Figure 1. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'Butterfly Artemis' after 2 and 3 weeks of vernalization during Experiment 1. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 2. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'La Belle White' after 2 and 3 weeks of vernalization during Experiment 1. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.


Figure 3. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'Tecolote Salmon' after 2 and 3 weeks of vernalization during Experiment 1. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 4. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'Butterfly Artemis' after 2 and 3 weeks of vernalization during Experiment 2. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 5. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'La Belle White' after 2 and 3 weeks of vernalization during Experiment 2. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 6. Effect of 12, 14, and 16-h photoperiod on days to visible bud (A), days to harvest (B), stem length (C), and stems harvested (D) of ranunculus (*Ranunculus asiaticus*) 'Amandine Black' after 2 and 3 weeks of vernalization during Experiment 2. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.

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CHAPTER 4

Short-day photoinductive cycles influence time to harvest, stem length, and morphology of dahlia specialty cut flowers

Short-day photoinductive cycles influence time to harvest, stem length, and morphology of dahlia specialty cut flowers

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Abstract

In the U.S. domestic market, dahlia (*Dahlia* \times *hybrida*) is a specialty cut flower that continues to increase in value. However, its availability is limited to late summer and early fall as it is classified as a facultative short-day (SD) plant and naturally flowers as the days become shorter toward the end of the outdoor growing season. Therefore, strategies to induce dahlia into flower under non-inductive natural long days in the field and greenhouse during early to midsummer are needed. The objectives of our study were to determine 1) the minimum number of photoinductive SD cycles required for flower bud initiation and development and 2) the impact of SD photoinductive cycles on time to harvest, stem length, and yield. Tubers of dahlia 'Jan Ryecroft', 'Karma Prospero', 'Linda's Baby', and 'Salmon Runner' were transplanted into bulb crates and placed in a greenhouse with a mean daily air temperature of 20 °C and a non-inductive 16 h long-day (LD) photoperiod for 7 weeks to promote vegetative growth. After 7 weeks under LDs, crates were placed under a photoinductive 9-h SD for 5, 10, 15, 20, 25, or 30 d, or were placed under continuous LDs or SDs. Crates were subsequently moved back to LDs after their respective SD cycles. Flower bud initiation occurred under all treatments; however, time to visible bud and time to harvest decreased as the number of photoinductive cycles increased. As the number of inductive cycles increased, stem length and caliper, and the number of lateral immature flower buds, decreased. The total number of stems harvested across all cultivars was lowest under continuous SD, while plants grown under all other treatments produced 92% more stems. Based on these results, we recommend growing dahlia cut flowers under LDs for 5 to 7 weeks to promote vegetative growth, followed by 10-15 photoinductive SD cycles for hastened flower initiation and time to harvest. To promote high-quality flower development and increased stem length, LDs should be provided for the duration of production.

Keywords: crop timing, flowering, limited inductive photoperiod, photoperiodism

Abbreviations: LD, long-day; LED, light-emitting diode; MDT, mean daily temperature; SD, short-day; SDP, short-day plant; TTH, time to harvest; TVB, time to visible bud

Introduction

In recent years, the domestic cut flower industry in North America has experienced a resurgence, with growers specializing in producing specialty cut flowers for local markets. From 2017 to 2022, wholesale domestic cut flower sales increased by \$90 million and the number of flower farms increased to approximately 10,800 in the United States (USDA, 2022). The specialty cut flower industry characteristically produces smaller quantities of flowers with a shorter vase-life and shorter potential storage duration compared to conventional, imported cut flowers (Darras, 2021). Therefore, some specialty cut flowers are not suited for long-distance transportation and are sold domestically (Wien and Pritts, 2008).

Dahlia (*Dahlia* ×*hybrida*) is a highly sought after specialty cut flower, due to the diversity found in the 20,000 available cultivars and their large, showy blooms (Armitage, 2008). Dahlia flowers have 29 forms (e.g. cactus, pompon, ball, etc.) and range in color and size, with diameters from 5-30 cm and colors including yellow, orange, red, pink, lavender, and bicolors (American Dahlia Society, 2023; Armitage and Laushman, 2003; Mariña, 2015). Dahlia cut flowers are typically grown from tubers that are propagated by division but can also be grown from seed or shoot-tip cuttings (Armitage and Laushman, 2003). According to the North American Specialty Cut Flower Production and Postharvest Survey, dahlia ranks among the five most common crops grown by cut flower growers in North America; however, 16% of respondents indicated that they experience a short postharvest lifespan of 4 or 5 d (Loyola et al., 2018).

Dahlias are classified as facultative and obligate short-day plants (SDP), meaning that flower induction is accelerated or only occurs under day lengths less than a critical duration, where the long dark period induces or accelerates flowering; however, some varieties are

classified as day neutral plants (Konishi and Inaba, 1964; Kumar et al., 1978; Runkle, 2003). Due to their long production time (~85 to 125 days to flower after planting) and sensitivity to frost, the harvest season is limited depending on the latitude and the region's environmental conditions (Burnett et al., 2023).

The influence of daylength on dahlia growth and development is well understood. Previous studies have determined that dahlia will flower under a wide range of daylengths, but flower bud initiation and development occur fastest when plants are grown under daylengths ≤ 10 h. For example, Konishi and Inaba (1966) reported that flower buds initiated under all photoperiods ranging from 8- to 16-h; however, flower bud formation was delayed as photoperiod increased. While flower initiation and development can be delayed under daylengths \geq 12 h, flowers will develop normally (Konishi and Inaba, 1966; Runkle, 2003). Some studies have reported that blind flower buds can develop when plants were grown under photoperiods \leq 12 h; this is due to the abortion of floral organs early in the stages of flower bud differentiation (Konishi and Inaba, 1966; Moe, 1971). Dahlias specifically grown as garden and potted plants have similar responses to photoperiod. Brøndum and Heins (1993) indicated that marketable D. pinnata 'Royal Dahlietta Yellow' plants with sufficient flower buds were produced under photoperiods of 12- to 14-h, while daylengths <12-h resulted in limited vegetative and reproductive shoot growth. Short days also hasten tuberous root formation as the shorter daylength serves as an environmental signal to store energy in the tubers (Legnani and Miller, 2001). The critical day length for tuberization is between 11- to 12-h, and tuberization under conditions <11 h will inhibit vegetative shoot growth (Moser and Hess, 1968; Legnani and Miller, 2001).

Similarly, Haliburton and Payne (1978) reported that days to flower bud initiation,

number of nodes, and overall height of dwarf-size *D. pinnata* 'Redskin' increased as photoperiod increased. It was suggested that high-quality potted dahlias could be produced by placing plants under a 9-h photoperiod to initiate flower buds and subsequently moved to a 13-h photoperiod for vegetative and reproductive development (Haliburton and Payne, 1978). Brøndum and Heins (1993) grew cutting-propagated dahlia 'Royal Dahlietta Yellow' at day and night temperatures ranging from 10 to 30 °C under photoperiods of 10 to 24 h to develop recommendations for potted production. Lateral shoot number under 20 °C and a 12- and 14-h photoperiod was ≈4 and ≈7, while plants under 15 and 25 °C and similar photoperiods produced ≈2 fewer lateral shoots. Lateral shoot length generally increased as photoperiod increased across temperatures. When considering vegetative shoot growth, reproductive timing, and plant height, it was recommended that plants should be produced at ~20 °C and under 12 to 14-h photoperiods (Brøndum and Heins; 1993).

Limited inductive photoperiod experiments, in which photoperiodic plants such as celosia (*Celosia argentea*), cosmos (*Cosmos bipinnatus*), coreopsis (*Coreopsis grandiflora; Coreopsis lanceolata*), strawberry (*Fragaria ×ananassa*), and marigold (*Tagetes erecta*) were moved from photoinductive to noninductive conditions have been performed to determine the minimum number of photoinductive cycles necessary for flower initiation (Damann and Lyons, 1993; Verheul et al., 2006; Warner, 2005; Warner, 2009). Additionally, the quantitative relationship between the number of inductive photoperiod cycles received and the strength of the flowering response have been reported (Verheul et al., 2006). For example, Warner (2009) placed *Celosia argentea* var. *plumosa* 'Gloria Scarlet' that had unfolded 1 to 5 leaf pairs under long-days (LDs) into inductive SDs for 5, 10, 15, 20, 25, or 30 d followed by LDs. Timing and duration of SD exposure interacted to influence the total number of inflorescences produced;

celosia plants became receptive to SDs 9 d after seedling emergence, and the minimum number of SDs necessary for flower induction was 6 to 9 d (Warner, 2009).

To reduce production timing for commercial dahlia cut flower growers and extend the harvest season, we quantified the minimum number of photoinductive SD cycles to initiate flower buds before transferring plants to non-inductive LDs. Therefore, the objective of this study was to determine 1) the minimum number of photoinductive SD cycles required for flower bud initiation and development of dahlia cut flower cultivars and 2) the impact SD photoinductive cycles have on cut flower time to harvest, stem length, and yield.

Materials and methods

Plant material

On 17 March 2023 (Rep. 1) and 27 February 2024 (Rep. 2) #1 size tubers of ball form dahlia 'Jan Ryecroft' and 'Linda's Baby', waterlily form 'Karma Prospero', and decorative form 'Salmon Runner' were received from a commercial distributor (Ednie Flower Bulb, Newton, NJ). They were planted into bulb crates (39.3 cm wide \times 59.7 cm long \times 17.8 cm tall; 0.23 m²) filled with 50:50 (v/v) commercial soilless medium composed of 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products Inc., Galesburg, MI) at a depth of 5 cm. Three tubers were planted in each crate and were spaced with 21-cm centers at a density of 13 tubers per m². These varieties were selected based on their diverse flower forms and popularity as specialty cut flowers.

Vegetative growth

The crates were placed in a glass-glazed greenhouse in the Plant Science Research Greenhouses at Michigan State University (lat. 43° N) with an air mean daily temperature set point of 20 °C (12 h/12 h day and night temperature of 22/18 °C). An aspirated thermocouple [20-gauge (0.151-mm diameter) type E_a Omega Engineering, Stamford, CT] positioned in the middle of each bench measured the canopy air temperature every 30 s, and a data logger recorded hourly means (Table 1). The greenhouse was equipped with exhaust fans, evaporative-pad cooling, radiant steam heating, and supplemental lighting controlled by an environmental control system (Integro 725; Priva North America, Vineland Station, ON, Canada).

Plants were grown under a 16-h LD to promote vegetative growth. The LD photoperiod consisted of a natural day length extended with supplemental lighting from high-intensity lightemitting diodes (LED) fixtures (GP-TOPlight DRW-MB; Koninklijke Philips N.V., Eindhoven, the Netherlands) between 0600 to 2200 HR. The LEDs provided a supplemental photosynthetic photon flux density of $\approx 125.4 \pm 12.6 \ \mu mol \cdot m^{-2} \cdot s^{-1}$ (mean \pm SD) [as measured with a quantum sensor (LI-250A light meter; LI-COR Biosciences, Lincoln, NE)] from 0800 to 1700 HR at plant height when the outdoor light intensity was below $\approx 440 \ \mu mol \cdot m^{-2} \cdot s^{-1}$ to achieve a mean DLI of $\approx 13 \ mol \cdot m^{-2} \cdot d^{-1}$. The 100-nm waveband ratios (%) emitted by the LED fixtures, defined by their blue (400-500 nm), green (500-600 nm), and red (600-700 nm) photon flux densities, were 12:7:81. Light intensity for each bench was recorded every 10 s with a quantum sensor (LI-190R; LI-COR Biosciences) positioned in the middle of the bench.

Inductive photoperiod greenhouse environment

After 7 weeks, crates under LDs were placed under a photoinductive 9-h SD for 5, 10, 15, 20, 25, or 30 days, or under control conditions of continuous SDs (9-h) or LDs (16-h). The SD photoperiod was created by opening and closing opaque black cloth over individual benches from 0800 to 1700 HR. When the nighttime air temperature on each bench fell under 19.8 °C, a 1500-W electric heater underneath each bench provided supplemental heating. The crates were subsequently returned to LDs after their respective SD treatment duration.

Plants were irrigated with MSU Orchid Reverse Osmosis (RO) Special [13N-3P-15K water-soluble fertilizer (mg·L⁻¹) 125 nitrogen, 13 phosphorus, 121 potassium, 76 calcium, 19 magnesium, 1.7 iron, 0.4 copper and zinc, 0.9 manganese, 0.2 boron, and 0.2 molybdenum; (GreenCare Fertilizers Inc.)] blended with RO water. One layer of 15-cm square supportive netting (HGN32804; Hydrofarm, Petaluma, CA) was secured \approx 60 cm above the crates. *Data collection and analysis*

Two stems from each plant per treatment were randomly selected and monitored daily for the presence of the first visible flower bud, open flower, and marketability (harvest), the date of each was recorded and time to visible bud (TVB), time to open flower, and time to harvest (TTH) were calculated. Dahlia stems were considered marketable and harvested once the inflorescence opened and petals were inverted past the centerline of the flower. Stems were harvested above the fifth node below the inflorescence to ensure consistency throughout harvest. Stem length from the base of the stem, stem caliper at the thickest point of the stem, and the number of lateral immature buds were recorded. Plants were monitored for 9 weeks to record the total number of marketable flowers each plant produced. The experiment used a randomized complete block design in a factorial arrangement and the experiment was replicated twice over time. Plants were blocked by treatment with 10 experimental units (individual plants) of each cultivar per treatment per replication. Bulb crates were randomly assigned to each photoperiod treatment which were randomized across benches within the greenhouse. Data were analyzed using SAS (version 9.2; SAS Institute, Cary, NC) mixed model procedure (PROC MIXED) for analysis of variance (ANOVA), and means were separated by Tukey's honest significant difference (HSD) test at $P \le 0.05$. There was a replication \times treatment interaction, therefore data are presented separately.

Results

Time to visible bud

Photoinductive SDs and replication influenced TVB of 'Jan Ryecroft', 'Karma Prospero', 'Linda's Baby', and 'Salmon Runner' (Table 2). Generally, TVB of 'Karma Prospero' and 'Salmon Runner' decreased as the number of SD cycles increased (Table 2, Fig. 2A and 4A). For example, during Rep. 1 and 2, TVB of 'Karma Prospero' grown under 10 and 30 SDs was hastened by 6 and 6 d, and 5 and 7 d, respectively, compared to those grown under continuous LDs (Fig. 2A). In contrast, TVB of 'Jan Ryecroft' and 'Linda's Baby' grown under continuous LDs was generally not different than plants grown under inductive SD cycles (Fig. 1A and 3A). *Time to harvest*

Regardless of treatment, all plants eventually flowered (data not presented). TTH of all four cultivars was influenced by photoinductive SDs and replication (Table 2). Generally, TTH of 'Jan Ryecroft', 'Karma Prospero', 'Linda's Baby', and 'Salmon Runner' in Rep. 1 and 2 was reduced by photoinductive SDs compared to plants grown under continuous LDs (Fig 1B, 2B, 3B and 4B). For instance, during Rep. 1 and 2., TTH of 'Karma Prospero' grown under 10 and 30 SDs was reduced by 8 and 12 d, and 8 and 14 d, respectively, compared to those grown under continuous LDs (Fig. 2B). Similarly, during Rep. 1 and 2, TTH of 'Jan Ryecroft', 'Linda's Baby', and 'Salmon Runner' was hastened by 7 and 10 d, 12 and 9 d, and 11 and 11 d, respectively, when plants received 30 photoinductive SDs compared to plants under continuous LD (Fig. 1B, 3B and 4B).

Stem length

The duration of photoinductive SDs and replication influenced the stem length of 'Jan Ryecroft', 'Karma Prospero', 'Linda's Baby', and 'Salmon Runner' cut flowers. Generally, stem

length was greatest under LDs and 5 SDs, while plants that received 30 or continuous SDs produced the shortest stems. During Rep. 1, 'Karma Prospero' plants grown under continuous LDs produced stems that were 33, 31, and 63 cm longer than stems under 15, 30, and continuous SDs, respectively (Fig. 2C). The stem length of 'Jan Ryecroft', 'Linda's Baby', and 'Salmon Runner' cut flowers followed similar trends (Fig. 1C, 3C, and 4C).

Cut flower morphology at harvest

For all cultivars tested, the number of photoinductive SD cycles and replication influenced the stem caliper of dahlia stem (Table 2). Usually, the thickest cut flower stems were those harvested under continuous LDs and 5 photoinductive SD cycles (Fig. 1D, 2D, 3D, and 4D). The stem caliper of 'Jan Ryecroft' grown under 5 SDs was 6.1, 5.6, and 5.7 mm thicker than stems grown under 20, 25, and 30 SDs, respectively, in Rep. 1 (Fig. 1D). Similarly, in Rep. 2, stem caliper of 'Karma Prospero' grown under 5 SDs were 3.5, 2.3, and 2.7 mm thicker than stems grown under 20, 25, and 30 photoinductive SDs (Fig. 2D).

The number of lateral immature flower buds per stem was also influenced by the number of photoinductive SD cycles and replication (Table 2). It was observed that there was a greater number of immature lateral buds on stems that were grown under \leq 25 photoinductive SD cycles. For example, during Rep. 2 'Salmon Runner' plants grown under 5, 10, 15, 20, and 25 photoinductive SD cycles produced stems with 5, 4, 3, 2, and 2 lateral buds, respectively; while those under 30 photoinductive SD cycles and continuous SDs produced 0 and 1 lateral buds, respectively (data not presented).

Total stems harvested

The total number of marketable stems harvested from each plant was influenced by the number of photoinductive SD cycles and replication (Table 2 and 3). In most instances, for all 4

cultivars, the greatest and fewest number of marketable stems were harvested under 5 photoinductive SDs and continuous SD, respectively (Tables 2 and 3). For example, under continuous SDs in Rep. 1 and 2, 'Linda's Baby' and 'Salmon Runner' produced 2.0 and 2.0 and 1.0 and 3.1 marketable stems, while under 5 SDs 'Karma Prospero' and 'Linda's Baby' produced 6.4 and 5.9 and 6.1 and 6.3 marketable stems, respectively, over a 9-week duration (Table 1 and 2).

Discussion

The results of this study support previous research which have reported that providing SDs can hasten flower induction (Damann and Lyons, 1993; Verheul et al., 2006; Warner, 2005; Warner, 2009), and therefore reduce TVB and TTH of dahlia. Additionally, providing a sequence of photoinductive SD cycles can influence flower morphology such as stem length and caliper, making stems more desirable for marketing purposes. Therefore, dahlia cut flower growers can provide limited inductive SD cycles using black cloth when the natural photoperiod is not inductive to harvest flowers earlier in the season, predict harvest windows, reduce overall production time, and improve quality of dahlia cuts.

Previous studies have indicated that daylengths <12 h inhibit vegetative shoot growth and increase abnormal flower development in dahlia 'Akane' and 'Futarishizuka', which were bred for cut flower production, while daylengths >13 h enhanced shoot growth and lead to normal flower development, though flower induction was delayed (Konishi and Inaba, 1964). Specifically, Konishi and Inaba (1966) reported that flower bud initiation occurred under daylengths of 8 to 16 h, though it was delayed as photoperiod increased. While flower development occurred and initiation was hastened under a photoperiod of \leq 10 h, the critical photoperiod to ensure normal flower development was 12 h. Likewise, Haliburton and Payne

(1978) reported that 100% of *D. pinnata* 'Redskin' grown under continuous 9-h SDs initiated flower buds, but under a 9-h photoperiod, plants did not receive sufficient photosynthetic light to promote normal growth and development. The present study supports these results as flower initiation occurred under both SD and LD photoperiods, but TVB of 'Jan Ryecroft', 'Karma Prospero', 'Linda's Baby', and 'Salmon Runner' grown under LD was delayed by 7, 14, 14, and 11 d compared to those grown under SD for the duration of the study during Rep. 1 and similar trends were observed during Rep. 2 (Figs. 1A, 2A, 3A, 4A).

There are many recognized forms of dahlia flowers, such as ball and pompon, cactus, decorative, dinner plate, and waterlily dahlias (American Dahlia Society, 2023; Burnett et al., 2023) and these different forms may demonstrate different responses to daylength. For instance, Yasuda and Yokoyama (1960) investigated the flowering response among different dahlia flower forms under LDs, natural daylength corresponding to 22 June (i.e. approximately 12.5 h), and an 8-h SD, and subsequently under different combinations of the above conditions. Pompon varieties-initiated flower buds in every treatment, while cactus and decorative varieties initiated 12 fewer flower buds under SD and natural daylengths, compared to pompon varieties. Our results support similar trends as 'Salmon Runner', a decorative form, initiated 30% more lateral buds under continuous LD conditions compared to continuous SD conditions, while 'Jan Ryecroft', a ball form, initiated a similar number of lateral buds under continuous LD conditions during rep. 2.

Plants grown under LDs following a photoinductive 9-h SD cycle produced more fully developed, marketable flowers compared to those receiving continuous SDs. These results are inconsistent with Yasuda and Yokoyama (1960) who reported that all dahlia forms receiving SD at any point in the study demonstrated higher flower bud and flowering percentages. Pompon

and decorative varieties grown under natural daylength conditions and moved to LDs, or plants grown under continuous LDs produced fewer flower buds and no open flowers after 60 d (Yasuda and Yokoyama, 1960). In the present study, plants exposed to continuous SDs produced fewer stems per plant compared to those under continuous LDs, aligning with the abovementioned Haliburton and Payne (1978) study. Similarly, Durso and Hertogh (1977) recorded lower flowering percentages and abnormal flower development for the garden variety *D*. *variabilis* under SDs. Forcing of 'Kolchelsee', a semi-decorative form, and 'Park Princess', a semi-cactus form, under an 8 h SD resulted in 0% and 78% of plants flowering, respectively.

While flowering of dahlia is delayed under continuous LDs, growing plants under LDs in combination with photoinductive SD cycles can ensure marketable stem lengths and strong stems for cut flower production (Konishi and Inaba, 1964; Legani and Miller, 2001). Legnani and Miller (2001) investigated the use of photoperiod manipulation for flowering and height control of dahlia plugs for potted production and reported that after being transplanted into a 13-cm container, plugs benefited from 1 to 2 weeks of SD to hasten flowering by 7 to 10 d and keep the plugs more compact, followed by LDs. In the present study, the dahlia cultivars tested benefited from the limited inductive SD exposure to induce flowering, followed by LD to ensure normal flower development, marketable stem lengths and greater stem caliper. For example, 'Karma Prospero' plants that were grown under 15 photoinductive SD for the entirety of the study.

Investigating the number of inductive photoperiod cycles has been critical to the production of several photoperiodic ornamental species. For example, Warner (2009) investigated the minimum number of SD cycles necessary for flower induction in *Celosia argentea* L. var. *plumosa* 'Fresh Look Red' and 'Gloria Scarlet', which are classified as

facultative SDPs. These two cultivars exhibited variation in the minimum number of SD cycles required and flowering was delayed when plants were moved back to LD after SD cycles compared to plants grown under constant SD. Similar to the present study, both cultivars produced more inflorescences when grown under a constant LD than under a constant SD; 'Gloria Scarlet' produced »21 and »7 inflorescence under LD and SD conditions, respectively (Warner, 2009). In the present study, dahlia plants continued to flower following photoinductive SDs regardless of the duration of SDs provided. Once transferred from inductive conditions, vegetative growth increased (i.e. stem length and stem caliper), though flower bud initiation and development continued. While TVB and TTH of plants receiving only 5 SD was delayed compared to longer SD cycles, for 'Karma Prospero' it was sufficient at accelerating flowering by 5 to 8 d compared to continuous LDs.

From a horticultural perspective, determining the critical number of inductive SD cycles for SDPs can reduce the amount of time under black cloth, thus reducing labor and overall production timing. Production of SDPs such as dahlias previously restricted to late summer and early fall can be extended by using photoperiod inductive cycle guidelines to produce dahlia cuts year-round. For example, if the natural photoperiod is <12 h, provide LD lighting for the first ~5 to 7 weeks of production to promote vegetative growth. When the natural photoperiod is >12 h, utilize black cloth to create SDs and therefore induce flowering. Ultimately, photoinductive cycle treatments enable growers to design production schedules that align with market demands, effectively reducing overall production time. In addition to influencing flower induction, transferring photoperiodic plants from SD to LD may influence stem elongation and contribute to the overall quality of the plant. The results of the study suggest that dahlia cut flowers should be grown under a combination of LD to SD to LD to achieve marketable cuts while reducing

TTH. Growing plants under LD will promote vegetative growth, followed by 10-15 SD inductive cycles for flower induction depending on the cultivar. After the SD cycle, plants should be provided with LD to promote stem elongation and increased inflorescence production

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Photoperiod	DLI	MDT (°C)	Day (°C)	Night (°C)				
	$(mol \times m^{-2} \times d^{-1})$							
)							
Rep. 1								
16-h entire duration	14.4 ± 6.2	19.5 ± 4.2	22.9 ± 2.6	17.4 ± 2.3				
(Continuous LD control)								
9-h entire duration	9.8 ± 3.5	20.9 ± 3.6	23.0 ± 2.9	17.7 ± 0.9				
(Continuous SD control)								
16-h bulking (before trts)	14.3 ± 3.0	20.2 ± 4.0	23.1 ± 1.8	17.4 ± 1.3				
5 short days	13.8 ± 5.2	20.6 ± 3.5	23.0 ± 0.7	18.2 ± 1.1				
10 short days	13.0 ± 5.5	19.1 ± 4.7	22.2 ± 1.9	16.2 ± 2.4				
15 short days	12.4 ± 1.3	19.7 ± 4.8	22.9 ± 2.0	16.7 ± 2.7				
20 short days	12.3 ± 4.1	19.7 ± 5.0	23.1 ± 1.7	16.4 ± 2.7				
25 short days	12.1 ± 2.2	19.7 ± 5.3	22.8 ± 3.0	17.0 ± 3.7				
30 short days	11.6 ± 1.0	20.3 ± 3.6	23.5 ± 2.6	17.0 ± 0.8				
Long day finish (after trts)	14.8 ± 4.1	20.0 ± 5.6	23.2 ± 3.2	18.7 ± 2.9				
	K	Rep. 2						
16-h entire duration	14.8 ± 5.1	19.7 ± 5.7	21.8 ± 3.1	17.6 ± 2.7				
(Continuous LD control)								
9-h entire duration	11.7 ± 4.3	20.5 ± 4.5	22.7 ± 1.7	18.4 ± 2.0				
(Continuous SD control)								
16-h bulking (before trts)	14.8 ± 5.1	19.2 ± 0.4	20.5 ± 1.9	17.9 ± 0.1				
5 short days	14.8 ± 5.6	19.4 ± 4.1	22.9 ± 0.8	16.2 ± 1.0				
10 short days	13.1 ± 5.5	19.1 ± 3.8	22.2 ± 1.4	16.1 ± 0.4				
15 short days	12.6 ± 5.0	19.4 ± 3.9	22.5 ± 1.6	16.3 ± 0.6				
20 short days	12.3 ± 5.4	19.0 ± 3.7	22.0 ± 1.5	16.0 ± 1.0				
25 short days	11.4 ± 0.4	19.1 ± 4.1	22.4 ± 1.7	16.8 ± 1.3				
30 short days	11.5 ± 3.4	18.9 ± 3.9	21.9 ± 1.5	16.0 ± 1.5				
Long day finish (after trts)	12.4 ± 4.3	20.5 ± 4.8	24.0 ± 2.1	16.9 ± 2.0				

Table 1. Mean daily light integral (DLI) [mean \pm SD], air mean daily temperature (MDT), day temperature, and night temperature [mean \pm SD] throughout the duration of dahlia finishing stages for Rep. 1 and 2.

	Days to visible bud (no.)	Days to harvest (no.)	Stem length (cm)	Stem caliper (mm)	Lateral buds (no.)	Total stems harvested per plant (no.)
			Jan Ryecroft			
Photoinductive (P)	**	***	***	***	***	*
Rep (R)	***	***	***	***	NS	*
$\mathbf{P} \times \mathbf{R}$	*	NS	***	NS	NS	NS
			Karma Prosper	0		
Photoinductive (P)	***	***	***	***	***	***
Rep (R)	***	***	***	***	***	***
$P \times R$	***	***	***	NS	**	**
			Linda's Baby			
Photoinductive (P)	*	***	***	***	***	***
Rep (R)	**	*	***	***	***	***
$\mathbf{P} \times \mathbf{R}$	NS	NS	***	***	NS	*
			Salmon Runner	<i>.</i>		
Photoinductive (P)	***	***	***	***	***	***
Rep (R)	***	***	***	*	***	*
$\mathbf{P} \times \mathbf{R}$	NS	NS	*	NS	NS	NS

Table 2. Analyses of variance for the effects of short-day (SD) photoinductive (P) cycles and replication (R) and their influence on time to visible bud, time to harvest, stem length and caliper, lateral buds, and total stems harvested per plant.

NS, *, **, *** Nonsignificant or significant at P £ 0.05, 0.01, and 0.001, respectively.

	Total stems harvested (no.)			
Treatments	Rep 1	Rep 2		
	Jan Ryecroft			
0 SD	2.8 a	4.0 a		
5 SD	2.9 a	5.4 a		
10 SD	3.1 a	3.2 b		
15 SD	2.6 a	2.6 b		
20 SD	2.3 a	3.0 b		
25 SD	2.5 a	2.5 b		
30 SD	2.7 a	2.9 b		
Continuous SD	1.9 b	1.9 b		
	Karma Prospero			
0 SD	4.2 a	5.5 a		
5 SD	6.4 a	5.9 a		
10 SD	3.1 b	4.4 a		
15 SD	2.1 b	4.7 a		
20 SD	3.7 b	4.7 a		
25 SD	3.2 b	3.8 ab		
30 SD	3.1 b	1.8 b		
Continuous SD	2.0 b	2.0 b		
	Linda's Baby			
0 SD	2.5 b	4.5 abc		
5 SD	6.3 a	6.7 a		
10 SD	1.8 b	6.4 ab		
15 SD	3.0 b	7.4 a		
20 SD	3.6 ab	6.3 ab		
25 SD	1.0 b	5.1 abc		
30 SD	2.6 b	3.7 bc		
Continuous SD	1.0 b	3.1 c		
	Salmon Runner			
0 SD	3.6 a	3.3 ab		
5	3.9 a	3.7 a		
10	3.2 a	4.3 a		
15	3.8 a	4.7 a		
20	3.0 a	4.0 a		
25	2.6 a	3.6 a		
30	2.1 a	2.7 ab		
Continuous SD	1.5 b	1.8 b		

 Table 3. Total stems harvested per plant and standard error of dahlia for Rep 1 and 2.

 Total stems harvested (no.)



Figure 1. Effect of continuous long days (LDs), 5-30 photoinductive short day (SD) cycles, and continuous SDs on days to visible bud (A), days to harvest (B), stem length (C), and stem caliper (D) of dahlia (*Dahlia* ×*hybrida*) 'Jan Ryecroft'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 2. Effect of continuous long days (LDs), 5-30 photoinductive short day (SD) cycles, and continuous SDs on days to visible bud (A), days to harvest (B), stem length (C), and stem caliper (D) of dahlia (*Dahlia* ×*hybrida*) 'Karma Prospero'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 3. Effect of continuous long days (LDs), 5-30 photoinductive short day (SD) cycles, and continuous SDs on days to visible bud (A), days to harvest (B), stem length (C), and stem caliper(D) of dahlia (*Dahlia* ×*hybrida*) 'Linda's Baby'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.



Figure 4. Effect of continuous long days (LDs), 5-30 photoinductive short day (SD) cycles, and continuous SDs on days to visible bud (A), days to harvest (B), stem length (C), and stem caliper (D) of dahlia (*Dahlia* ×*hybrida*) 'Salmon Runner'. Letters indicate mean separation across photoperiod treatments using Tukey-Kramer difference test at $P \le 0.05$. Error bars indicate standard error.

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