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Review paper

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The habit of strawberry flowering is the key for runner propagation, where the photoperiod is the main environmental factor - A review

I.A.H. Al-Madhagi
Department of Horticulture and Its Technologies, Faculty of Agriculture, Foods and Environment, Sana'a University, Sana'a, P.O. Box 1247, Yemen.

Key words: Chilling, division, flowering, *Fragaria x ananassa* Duch, gibberellin, photoperiod, proliferation.

[*] **Corresponding author:**
isam.madhagi@gmail.com
i.madhagi@su.edu.ye

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Abstract: Despite the advancement of tissue culture in strawberry plant propagation, the degree of elite for field cultivation depends on forcing the plant to produce runners. The strawberry flower habit [everbearing (EB), seasonal berry (SB), short-day (SD), long-day (LD), and day-neutral (DN)] defines the method of encouraging the plant to generate runners, since the formation of runners is mostly influenced by genetic factors before being influenced by environmental factors. Stolon production, which occurs as a result of vying for resources under certain environmental circumstances, is the reverse of blossoming. Therefore, any stimulus that encourages stolon formation and vegetative growth limits the development of flower buds, which is necessary for elite propagation. Long photoperiod, temperature, chilling hour, or cold storage, and plant growth regulators (PGR) are cited as these variables. Temperature has a significant impact on runner development, although the long daily photoperiod (LD) remains the most crucial component in runner induction. However, when LD interacts with other factors like temperature, cold storage, and gibberellins, its efficiency is increased. Thus, based on the cultivars and the seasonal climate of the geographical location, the best approach for strawberry propagation is identified by optimising the planting date for propagation or adjusting the propagation circumstances.

1. Introduction

Strawberry (*Fragaria x ananassa* Duch) is a commercial crop grown worldwide for its nutritional and health benefits. Strawberries are consumed as fresh fruit or juice, or processed industrially into jam used in a various of desserts such as candy, milk and ice cream. According to the FAO statistics service agency (FAO, 2021), strawberry production has increased significantly over the past half-century (from 1960 to 2021). The total global production in 2021 is estimated to be around 9,175,384.43 t, with a cultivated area of about 389,665 ha. China contributes for approximately 37% to global production, while the Arab nations contribute only 6%, with Egypt, Morocco, and Jordan making up the majority.

The development of strawberry production in various countries depends on the selection of the most suitable cultivars for their annual climate. Vegetative propagation is the ideal technique for strawberry propagation since it retains the mother's characteristics (Li *et al*., 2020). Strawberry nurseries, as a result, play an important role in the expansion of strawberry cultivation within a specific geographical area. It is critical for commercial plant production to select the best factors to stimulate the plant to produce runners.

In this review, the vegetative growth of strawberry plants will be covered as a technique for containing blossoms and encouraging the plant to generate runners. Blossoming and the development of runners are mutually exclusive. Flowers must be controlled in the practical application of runner production, either by eliminating the flowers or by altering the environmental conditions. Long photoperiods (DL) and high temperature (HT) are crucial for promoting stolonization (Smeets, 1955; Smeets and Kronenberg, 1955; Went, 1957; Leshem and Koller, 1965; Smeets, 1980), which is related to increased gibberellin production (Tafazoli and Vince-Prue, 1978). In addition, cold storage of plants promotes the production of runners (Hamano *et al*., 2009; Watanabe *et al*., 2009; Al-madhagi *et al*., 2018). Exogenous application of growth regulators such as gibberellins, cytokinins or their combination supports the development of the runners (Kender *et al*., 1971). Long photoperiods (LD) are the most essential factors for runnering induction in strawberry, but its effectiveness is enhanced by its interaction with other factors such as temperature, cold storage, and gibberellins.

Within this context, the primary goal of this paper is to present an overview of the factors that influence strawberry runner yield.

Strawberry flowering habit and cultivars division

Genetics is the primary component governing strawberry proliferation. Moreover, it pinpoints the best techniques as well as the coefficients of the propagation means. Since *F. ananassa* Duch, the cultivar of the strawberry, is a hybrid plant, the variations in strawberry cultivars may be attributed to variations in its fundamental parents, *F. virginiana* and *F. chiloensis*, each of which has a unique blooming and runnering behaviour. *F. chiloensis* began to bloom before *F. virginiana* and its majority of the leaves stayed evergreen throughout the winter. In the meantime, genotypes of *F. virginiana* seemed to become dormant, and their leaves became brown and withered off in the late fall and winter, outperforming *F. chiloensis* for runner production (Darrow, 1966; Hancock *et al.*, 2003).

The capacity of the bud in cultivars to continue producing inflorescences throughout the growing season accounts for the variation in runner development. According to other researches (Guttridge, 1985; Hytönen and Elomaa, 2011), this is connected to the differentiation of the meristem into a leaf rosette, also known as a branch crown or stolon. A branch crown serves as a platform for inflorescences, whereas a runner is a vegetative, extended shoot with a terminal daughter plant that may be employed for clonal multiplication (Samad *et al*., 2021).

Based on physiological and production features, strawberry plants were split into various classes. As seen in figure 1, each group has a specific function, one for physiological characteristics and the other for productive attributes. Because they influence planting and harvesting dates, as well as seedling reproduction and harvesting techniques, physiological features are important. For both fresh and processed products, the production features (qualitative and quantitative) are essential to satisfy local consumers' needs and exporters' demands.

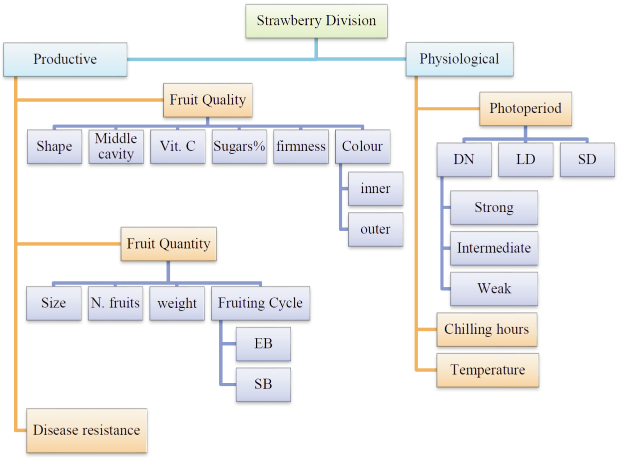

Fig. 1 - A list of different features that can be taken into account to describe a strawberry cultivar and eventually classify it. Strawberry cultivars are classified into physiological and productive traits, with physiological traits playing the most important role in determining runner performance and productivity. SD: short-day, LD: long-day, DN: day-neutral, EB: everbearing, SB: seasonal berry.

Based on how they react to the photoperiod for flower induction, strawberry cultivars are categorised as short-day (SD), long-day (LD), or day-neutral (DN) (Durner *et al*., 1984). The ideal method for plant multiplication, blooming behaviour, and fruit production is determined by this division, which is crucial. In the meanwhile, strawberry cultivars exhibit considerable addiction as a result of interactions between photoperiodic temperature. This link has led to the interchange ability of the two terms when describing strawberry blossoming behaviour (Cai *et al*., 2017).

Based on their respective production periods, strawberry cultivars were divided into two groups: everbearing (EB) and seasonal berry (SB). This division may be thought of as an implementation of actual cultivar behaviour in response to temperature and photoperiod. While certain places of the world may only see one season of production from different strawberry SB kinds, other locations may experience two seasons. As a result, the split of production cycles is inaccurate globally while being based on the same latitude (Table 1).

The major gene that regulates blooming and runner production is called Perpetual Flowering Runnering (PFRU) (Hytönen and Kurokura, 2020). Retentive, day-neutral (DN), continuous flowering, and long-day plants are all examples of everbearing (EB) cultivars (Cai *et al*., 2017). The words "day-neutral" (DN) and "everbearing" (EB) are interchangeable and refer to a physiological insensitivity to day-duration in flower bud initiation and a realistic expectation of strawberry producing. Weak, moderate, and strong day-neutral cultivars can be used to categorise the everbearing strawberry cultivars (Nicoll and Galletta, 1987).

EB cultivars can produce multiple crops throughout the year, regardless of day length, at a significantly higher temperature than seasonal berry (SB) cultivars (Smeets, 1980).

Everbearing (EB) strawberry cultivars, in contrast to SB strawberry cultivars, have been linked to early flowering and initiation at shoot tips, resulting in better crown branching ability (Hytönen and Elomaa, 2011). As a result, EB strawberry cultivars tend to produce few stolons on a large scale (Darrow, 1966; Simpson and Bell, 1989; Dale *et al.*, 1996), and fewer stolons than SB. Since branch crowns are ended by inflorescences, the quantity of branch crowns is essentially correlated with the quantity of inflorescences (Hytönen *et al*., 2004; Tenreira *et al*., 2017).

In the meanwhile, branch crowns that form from buds in the leaf axils of the crowns of mature plants are divided to create economically viable EB strawberry plants. The EB strawberry cultivars are quantitative LD plants at medium temperatures, day neutral only at low temperatures (15°C), and qualitative LD plants at high temperatures (Pedraza *et al*., 2010; Samad *et al*., 2021). Short-day (SD) conditions, as seen in figure 2, cause EB cultivars to stop growing and become dwarfed throughout the summer season (Darrow and Waldo, 1934). For growth, bloom initiation, and stolon formation in EB strawberries, a critical photoperiod of 15 hours at 18°C and 14 hours at 30/25°C day/night temperature is needed (Nishiyama *et al*., 2006; Sønsteby and Heide, 2007).

Seasonal strawberry blooms (SB), which bloom in the spring and produce a fruiting crop in the summer, have been identified as short day (SD), once blooming, seasonal flowering (SF), seasonal berry (SB), single crop, or June-bearing plants (Cai *et al*., 2017). In

Table 1 - Shows the differences in runnering and cropping between Everbearing (EB) and Seasonal blooming (SB) strawberry varieties throughout the year

Type	Defined	Cropping over the year	Runnering	Commercially propagated
Everbearing (EB)	Remontant day-neutral (DN) perpetual LD plants	A couple of crops	Only non- to a few runners	Dividing of branch crowns
Seasonal flowering (SB)	once flowering seasonal flowering (SF) seasonal berry (SB) single cropping June-bearing short-day (SD)	One fruit crop	More runner	From the plantlets

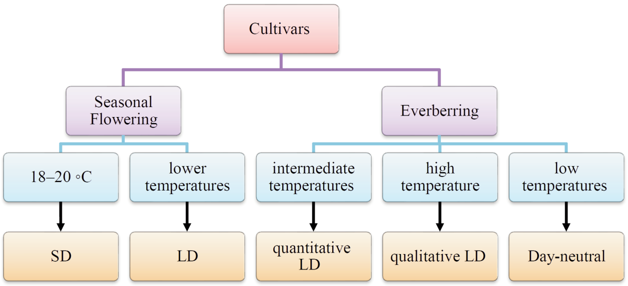

Fig. 2 - A schematic diagram shows the flower habit of strawberry cultivars that flower all year round is the key to propagation. Where: Everbearing (EB) behave as day-neutral (DN) plants at low temperature and are considered qualitative long-day (LD) at medium temperature and quantitative long-day (LD) at high temperature. Seasonal Flowering (SF) behave like long-day (LD) at lower temperature and like short-day (SD) at medium temperature.

response to the seasonally reducing photoperiod and temperature circumstances, SB strawberries begin to bloom in the late summer and fall, the year before blossoming and fruiting. The majority of SB cultivars are now regarded as facultative short-day (SD) plants as it has been established that they are mostly SD plants. At temperatures between 18 and 20 °C, they need SD for bloom induction, although at lower temperatures, the majority of cultivars begin flowering on long days (LD) (Ito and Saito, 1962; Heide, 1977; Heide *et al.*, 2013).

The crucial photoperiod for SD induction is 14–15 hours (Darrow and Waldo, 1934; Konsin *et al.*, 2001) and the minimum number of SD cycles required for induction depends on the cultivar (Heide *et al.*, 2013). The flower-inducing effect of SD, on the other hand, is temperature sensitive, peaking at intermediate temperatures and decreasing rapidly at temperatures above 21°C (Heide *et al.*, 2013).

2. Propagation of strawberry

SB strawberry plants are commercially propagated from plantlets that multiply from the runner nodes of mature plants because technique is quicker than seed propagation and daughter plants retain the traits of their mother plant (Li *et al.*, 2020). This plantlet is often created by nodes borne by runners or stolons that sprout from buds in the crown's leaf axils over the summer (Darrow, 1966). The runners often is elongated branch which have nodes and internodes running parallel to their length, with the bud at the first node usually being inactive (Ahmed and Ragab, 2003). It's length is due to the cell division and intermodal elongation in the plant are responsible for runner growth (Nishizawa and Hori, 1993). Therefore, one of the most important metrics is the number of runner and daughter plants produced by mature plants.

3. Environmental factors

The environmental conditions are one of the most crucial factors impacting the generation of strawberry runners. In all of the *Fragaria* genotypes examined, stolon formation and flowering induction can compete for space in the axillary meristems, and both developmental strategies are sensitive to environmental factors (Brown and Wareing, 1965; Guttridge, 1985; Bradford *et al.*, 2010; Hytönen and Elomaa, 2011; Heide *et al.*, 2013; Hytönen and Kurokura, 2020). In response to any alteration in the environment that encourages flowering (flowering habit), the strawberry produces a crown or stolon (Fig. 2). The photoperiod, chilling periods, and temperature are especially linked to these environmental or seasonal factors, and their interactions may have a major effect on strawberry dispersal (Andrés and Coupland, 2012; Salinas *et al.*, 2017).

Photoperiod

Photoperiod is the duration of the daily exposure of an organism to illumination within hour (Cammack *et al.*, 2008), it is defined as the period of time within a 24-hour time frame that light is available (Lanoue *et al.*, 2019).

One of the most crucial environmental factors for plants is light. Where, the plant is impacted by the length of the lighting period (photoperiod), the radiation strength, and the type of illumination wavelengths (colours). Plants employ photosynthesis, a process that uses light as an energy source, to produce secondary compounds and carbohydrates. Additionally, photoreceptors produce light that is utilised to detect and keep track of environmental changes (Chen *et al.*, 2004). When it comes to the photoperiodic control of flowering in wild strawberries, phytochromes are crucial photoreceptors (Rantanen *et al.*, 2014).

The photoreceptors' main module, the leaves, is capable of detecting a broad range of wavelengths, light intensities, and photoperiods. It controls the essential gene proteins that the plant's developmental regulatory programme may use to transmit information about timing and light (Valverde, 2011; Shim *et al.*, 2016). Photoreceptors also enable plants to accurately monitor ambient light conditions and alter their development, morphology, and metabolic rates, including the start of blooming, in accordance with the particular environment in which they exist (Song *et al.*, 2018; Roeber *et al.*, 2022).

FLOWERING LOCUS T (FvFT1) and SUPPRESSOR OF THE OVEREXPRESSION OF CONSTANS1 (FvSOC1), two significant genes in the photoperiodic regulation of blooming and runners in woody strawberries, have provided some information on the photoperiodic control of FvTFL1 in seasonal flowering woodland strawberry. FvTFL1 integrates photoperiod and temperature signals to control flower induction, and higher FvFT1 mRNA levels are linked to earlier flowering under a variety of environmental conditions including light quality, photoperiod, and temperature, while turning off this gene significantly delays flowering (Hytönen and Kurokura, 2020).

The long-day photoperiod (LD) is one of the most important environmental elements affecting the growth and development of strawberries (Ito and Saito, 1962; Darrow, 1966; Heide, 1977; Okimura and Igarashi, 1997; Robert *et al.*, 1999; Heide and Sønsteby, 2007; Al-madhagi *et al.*, 2011; Hasan *et al.*, 2011; Li *et al.*, 2020). And in distinguishing strawberry runner axillary buds (Hytönen *et al.*, 2009).

The effect of photoperiod on strawberry vegetative development and runner production has been widely discussed and has attracted the attention of numerous studies. Petioles length, leaf number, leaf area, and runner number and length all increase with LD photoperiod (Darrow, 1966; Sung, 1973; Plancher and Naumann, 1978; Nishizawa and Hori, 1993; Pipattanawong *et al.*, 1996; Robert *et al.*, 1999; Wiseman and Turnbull, 1999; Konsin *et al.*, 2002; Serçe and Hancock 2005; Sønsteby *et al.*, 2006; Hasan *et al.*, 2011; Li *et al.*, 2021 b). LD conditions promote cell division and cell elongation (Nishizawa, 1992; Nishizawa, 1994), due to an increase in the amount of endogenous gibberellins (GAs) that promote bud development in the plant (Taylor *et al.*, 1994).

The number of hours during the LD photoperiod that the plant must be urged to produce a runner depends on a variety of factors, including cultivars and temperature. The photoperiodic cycle of 10 h light and 10 h dark failed to develop runners, but 14 h light and 14 h darkness did, and runner plants growing in LD were induced to flower provided they remained connected to parent plants growing in SD (Hartmann, 1947). As shown in figure 3, the impact of photoperiod (P) on strawberry propagation depends on a number of different parameters, including cultivar (C), cold storage (CS), temperature (T) and plant growth regulators (PGR).

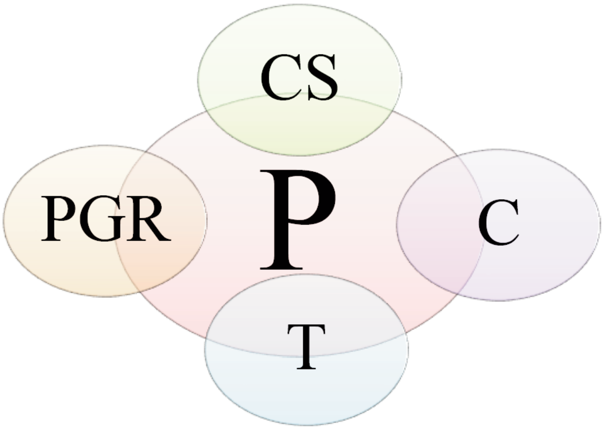

Fig. 3 - The response of strawberries to the photoperiod (P) effect on runner development is influenced by a number of other parameters, including cultivar (C), cold storage (CS), temperature (T), and plant growth regulators (PGR).

Photoperiod × cultivars (P×C)

The number and length of runners was influenced not only by photoperiod but also by cultivars or genetics, and the interaction of the two (Pipattanawong *et al.*, 1996; Serçe and Hancock 2005; Hasan *et al.*, 2011). In terms of runner production, the strawberry parents responded differently to the photoperiod.

The study by Serçe and Hancock (2005) shows the different responses of the wild strawberry genotype, *F. chiloensis* 'CFRA 0024' (Central Chile) and 'CFRA 0368' (Alaska) and *F. virginiana* 'Eagle 14' (Ontario); they just found that only 'Eagle 14' and 'CFRA 0368' produced an appreciable number of runners while 'Eagle 14' did not show a consistent trend, while 'CFRA 0368' had the most runners under the 11 hour photoperiod.

Clear photoperiod responses to vegetative development and stolon production were observed in SB cultivars (Plancher and Naumann, 1978; Konsin *et al.*, 2002; Sønsteby *et al.*, 2006; Hasan *et al.*, 2011), as well as on EB strawberry cultivars (Guttridge, 1969; Dennis *et al.*, 1970; Serçe and Hancock, 2005).

The difference between EB strawberry cultivars is also evident: cultivars 'Aromas', 'Tribute', 'Frederick 9', and 'Fort Laramie' did not produce runners under either LD (16h) or SD (8 h), but 'Quinalt' produced 0.2 runner/plant under LD (16h) (Serçe and Hancock, 2005). Flower initiation and runner development occur independently of LD in EB strawberry cultivars (Piringer *et al*., 1958; Piringer and Borthwick, 1961; Guttridge, 1969; Dennis *et al*., 1970).

There was also a difference between SB cultivars, where 'Camaroga' yielded the most plantlets (22.06 per plant) when grown under the 17 hour photoperiod (Hasan *et al*., 2011).

According to Serçe and Hancock (2005), the LD photoperiod had a significant effect on runner production, with a significant effect of an interaction between the SB cultivar and the photoperiod, with 'Allstar' and 'Honeoye' not producing runners in photoperiod ranges of 8 -11 h, and 'Chandler' producing runners in photoperiod ranges of 8 , 9, or 11 h.

Strawberry SB developed more crowns than runners during the SD photoperiod compared to the plant under the LD (18 h) photoperiod on the 'korona' SB strawberry (Konsin *et al*., 2001). The number of runners is also differs between cultivars, in strawberry 'Seolhyang' it increased dramatically after LD (16 h) (Li *et al*., 2020). Meanwhile, for SB 'Camarosa' and 'Camaroga' cultivars, there was no significant difference between the 15 h and 17 h LD photoperiods, and the LD (15 h) was determined to be extremely efficient (Hasan *et al*., 2011).

Temperature (T)

Strawberry flowering habits (EB or SB) have been found to be under either qualitative or quantitative genetic influence (Heide *et al*., 2013). Figure 2 shows the behaviour of strawberries under different temperature conditions.

Wherever, the value of 10°C is a base temperature of strawberries (Al-madhagi *et al*., 2018). In *Fragaria vesca*, higher temperatures were found to be critical for runner induction (Heide and Sønsteby, 2007). The temperature variation between day and night at the same average daily temperature is also significant in creation runners; in strawberry 'Seolhyang', 25/15°C day/night was the best temperature for runners formation (Li *et al*., 2020).

LT (11°C) and SD (10 h) enhanced branch crown growth in wild strawberry *Fragaria vesca*, but HT (>18°C) promoted runner initiation independent of photoperiod (Bedry, 2017).

Regardless of temperature, all of the *F. x ananassa* EB cultivars showed very low runner counts. Temperature has an effect on runner formation in EB strawberries (Smeets, 1955; Smeets and Kronenberg, 1955; Serçe and Hancock, 2005). Controlling temperature alone, as well as cultivating plants at varied temperatures, will not increase EB strawberry runner output (Samad *et al*., 2021).

The EB cultivars responded differently to temperature in terms of runner production, with the greatest number of runner being 0.6 and 0.7 at 30°C in 'Aromas' and 'Tribute,' respectively. In contrast, below the T- range of 18-30°C, neither 'Ogallala' nor 'Quinalt' produced a runner (Serçe and Hancock, 2005).

A recent study Samad *et al*. (2021) found that runner production in EB strawberries decreased significantly at 20°C, with no statistical difference between 25 and 30°C. Runners was almost twice in EB strawberries 'Murano' than in 'Favori' during the season and it was significantly higher in the plants raised outdoors than in those raised in the greenhouse (Sønsteby *et al.*, 2022). The explanation for this is that EB's runner potential is cultivar dependant, and low temperatures (LT) put more energy into flowering than runner development (Rivero *et al.*, 2021 a; Sønsteby *et al.*, 2021).

Photoperiod × temperature (P×T)

Overall, the effect of photoperiod on runner and crown production was influenced by temperature at the time of photoperiod application. LD and high temperature (HT) have been shown to improve runnering in all flowering classes of strawberry cultivars (EB or SB) (Serçe and Hancock, 2005). When the photoperiod was 12 h or more and the temperature was above 10°C, runners began to multiply (Went, 1957; Darrow, 1966).

The strawberry's reaction to the photoperiod is affected by temperature (Darrow, 1936). Actual photoperiod and temperature parameters varied by cultivar (Went, 1957). The LD must exceed a certain value at HT for runner development in EB and SB strawberry cultivars (Darrow, 1937; Went, 1957; Smeets, 1980). Temperature and photoperiod promote runnering by inhibiting flower initiation and increasing the activation of vegetative buds on the rosette crown (Went, 1957; Leshem and Koller, 1965). Meanwhile, there was no runner development at SD LT, and LT at higher light intensities had to be suppressing flower initiation (Went, 1957). Strawberries can develop runners at a higher temperature than at a lower temperature (Smeets, 1955; Smeets and Kronenberg, 1955; Went, 1957; Leshem and Koller, 1965; Smeets, 1980).

The ideal temperature for strawberries varies by cultivars. Under both LD and SD photoperiods, strawberry cultivars differ in the optimal temperature for runner development, and the number of runners produced increased as the temperature rose from 20 to 26°C under 16 h LD, but decreased as the temperature increased from 26 to 29°C (Bradford *et al*., 2010).

EB produced many runners during the 15 h - 20 h LD photoperiod with a temperature of at least 22.7°C (Darrow, 1966; Rivero *et al.*, 2021 a), no runners developed in 'Marshall,' at 10°C but did for 16 hours at 14°C, and for 12 hours at 17°C (Went, 1957). When the temperature dropped to 18°C, the LD photoperiod factor alone was sufficient for optimal leaf and inflorescence growth and development (Sønsteby *et al.*, 2006). Photoperiod preconditioned plants produced significantly more branch crowns than control plants, but cold-stored tray-conditioned plants produced much fewer crowns (Sønsteby *et al.*, 2006).

A LD of at least 14 hours was required for runner production in 9 cultivars cultivated at 13, 16, and 21°C in EB strawberry cultivars, where the photoperiod LD up to 14 h being the key determinant, a specific temperature being required for a prolonged runner development duration (Darrow, 1936). Flower initiation and runner formation in 'Revada' and 'Rabunda' occurred at 20 and 26°C regardless of the LD, and the length of runner formation was longer at 20 and 26°C than at 14°C, and at 16 and 24 h than at 8 h (Smeets, 1980).

Runners are formed almost entirely in the vegetative phase of plant growth in SB cultivars, with LD × HT favouring runner production (Darrow and Waldo, 1934; Heide, 1977; Durner *et al*., 1984; Bradford *et al.*, 2010). SB cultivar also behaves like EB plants at LT under LD circumstances (14 h) (Darrow and Waldo, 1934; Darrow, 1936). The Honeoye SB cultivar did not develop runners at 14 or 17°C, regardless of photoperiod, and it did not produce runners under SD, independent of temperature (Bradford *et al*., 2010). In the number of runners of F1-hybrid 'Delizzimo' cultivar was significantly higher at 26°C than at lower 12°C under both SD and LD conditions (Samad *et al.*, 2022). Addition, higher temperatures increased the concentrations of sugars in the leaves in LD photoperiod (Rivero *et al.*, 2022).

The EB trait can also arise when inflorescences are removed during the growing season, leading to the development of latent buds, as in the LD and HT traits causing flowering suppression (Sugiyama *et al.*, 2004). As shown in Table 2, the runner formation rises at HT × LD in both SB and EB.

Table 2 shows a rough summary of the influence of photoperiod and temperature interaction on the generation of runners. Despite the fact that the critical value of each variety is different, both groups agreed that the long day (LD) at high temperature is the best condition for the development of runners.

Chilling hour and cold storage (C)

Flower initiation in strawberries requires chilling (Ito and Saito, 1962; Darrow, 1966; Kinet *et al.*, 1993; Lieten, 1997; Al-madhagi *et al.*, 2018; Al-doubibi *et al.*, 2021). For the best production and berry quality, both types of strawberries (EB and SB) required different amounts of chilling period before planting. The chill-hours are measured in degrees below than 5, 7, or 8°C (Yanagi and Oda, 1993; Risser and Robert, 1993; Bigey, 2002; Gallace *et al.*, 2019). If the natural environment is not favourable, the refrigerator can be used to carry out cold treatments (Hamano *et al*., 2009). Chilling stimulates cell division and elongation by breaking dormancy (Lee *et al*., 1970; Yanagi and Oda, 1989).

The effect of chilling (up to zero and less than 5°C) or cold storage (below zero °C) on runner development has been connected to the type of strawberry (EB or SB), cultivars, degree of chilling, length of cold storage, and cumulative of natural chilling hours, according to the most recent study.

Longer cold treatments (more than 500 hours) limit flower development (Taghavi and Aghajani,

Table 2 - Interaction effect of photoperiod and temperature on runnering of strawberry

Factors		Cultivars	
Photoperiod	Temperature	EB	SB
SD*	Low	×	×
LD	Low	Some cultivars	×
DN	Low	×	×
SD	high	×	×
LD	high	√	√
DN	high	Some cultivars	√

*SD (short-day) is less than 14 hours, LD (long day) is more than 14 hours, and DN (day-neutral) is 12 hours. √: producing runner, ×: non-producing runner. Low= less than 20°C.

2017), lead to the shorter flower differentiation (Lieten, 2006; Al-madhagi *et al.*, 2018) and delay the re-initiation of fresh floral primordial in the spring (Guttridge, 1958; Gallace *et al.*, 2019). Strawberry propagation could benefit from this approach.

Chilling has been shown to increase runners generation in both EB and SB strawberry cultivars (Yanagi and Oda, 1990). Many runners were formed when the strawberry EB or SB cultivar was subjected to a lot of cooling hours (Bringhurst *et al.*, 1960; Bailey and Rossi, 1965; Guttridge, 1969; Braun and Kender, 1985; Kahangi *et al.*, 1992; Risser and Robert, 1993; Lieten, 1997; Tehranifar *et al.*, 1998; Bigey, 2002; Hokanson *et al.*, 2004; Taghavi and Aghajani, 2017; Al-madhagi *et al.*, 2018).

The sensitivity of the chilling duration varies between cultivars; SB strawberry cultivars are more sensitive than EB cultivars, and prolonged chilling inhibits blossom production in SB cultivars (Yanagi and Oda, 1990).

After more than 1000 hours of chilling, EB cultivars formed runners (Hamano *et al.*, 2009; Watanabe *et al.*, 2009; Al-madhagi *et al.*, 2018). Although the cultivar does not develop runners under normal conditions, and does not produce runners when chilled for 0 h, 360 h and 720 h, long chilling hours (1080 h and 1440 h) in a cold room at 2°C will reduce the flower and promote more runner (Al-madhagi *et al.*, 2018). For Japanese EB strawberry cultivars (‘Akihime’, ‘Askaruby’, ‘Sachinoka’, ‘Tochiotome’, ‘Toyonoka’, ‘Nyoho’, and ‘Yumenoka’), cold storage for more than 1000 hours interrupts dormancy, promotes runner development, and increases leaf elongation (Watanabe *et al.*, 2009).

The duration of the cooling period for current EB strawberries is related to the cultivars. Chilling temperatures in EB cultivars start with runner development in ‘Revada’ and ‘Rabunda’ cultivars that have not experienced natural hours of chilling (Smeets, 1980), as well as in ‘Rabunda’, ‘Ostara’, and ‘Kletter’ cultivars refrigated at 1°C for 1 and 2 months (Yanagi and Oda, 1990).

Flowering degree and stolon production in EB strawberry cultivars Delizzimo and Favori had little or no effect when chilled at 2°C for six weeks (Rivero *et al.*, 2021 a). Furthermore, for a one to four weeks of chilling at 1°C increased runners in the cultivar EB ‘Pajaro’, with no significant difference in the length of cold storage, while one or two weeks of cold storage resulted in a larger number of daughter plants (Taghavi and Aghajani, 2017).

Longer cold storage duration improved runner production in the SB strawberry cultivars ‘Hokowase’ (Yanagi and Oda, 1990), ‘Korona’ and ‘Elsanta’ (Sønsteby and Heide, 2006), ‘Allstar’, ‘Chandler’, ‘Latestar’, ‘Northeaster’ and USDA selection B27’ (Hokanson *et al.*, 2004) and ‘Sulhyang’ (Lee *et al.*, 2020).

SB strawberry cultivars stored chilled at 1°C for two months produced more runners than fresh plants that had never been exposed to cold (Hokanson *et al.*, 2004). The degree of cold storage also influences runner quality. According to (Lee *et al.*, 2020) Sulhyang’ plants held at -5°C produced fewer daughter plants than those stored at -2°C, and the quantity of daughter plants was modest.

Long cold storage reduced vigour and glucose stores of mother plants (Lieten *et al.*, 1995). Plants that have been stored cold for a long period should have a higher starch content and if possible, be cultivated in nurseries located at higher altitudes (López *et al.*, 2002; Al-doubibi *et al.*, 2021). On the other hand, naturally cool night-time temperatures at higher elevations help plants collect more starch. The quantity of chilling hours the plant experiences affects runner production; both insufficient chilling and excessive chilling have an effect (Hamano *et al.*, 2009).

Photoperiod × cold storage (P × C)

As a result, exposure to prolonged photoperiods and longer cold storage duration improved runner production. The results of the previous study show that cultivars respond differently to photoperiod × cold storage and duration. After determining the cultivar type (EB or SB), this interaction is linked to the length of cold storage LC and LD photoperiod (Sønsteby and Heide, 2006; Hamano *et al.*, 2009; Watanabe *et al.*, 2009; Rivero *et al.*, 2021 a). Due to its insensitivity to the pre-chilling history and day duration, the EB strawberry ‘Rabunda’ showed consecutive flower development (Yanagi and Oda, 1989).

Meanwhile, more efficient runners production can be achieved in EB strawberry cultivars by combining cold storage with LD photoperiod, where LD (16 h) increase runner production by about 10% in plants chilled at 4°C that for 1000 and 1500 hours in comparison to unrefrigerated ones (Watanabe *et al.*, 2009). The same result was observed in EB strawberry ‘Natsuakari’ and ‘Dekoruju’ treated with 1000 h chilling under 16 h LD (Hamano *et al.*, 2009). EB strawberry cultivars ‘Natsuakari’ and ‘Dekoruju’ chilled for 1500 and 2000 hours (5°C) produced runners above natural day length, but not below natural day length regardless of LD treatment.

In contrast, after 5 and 10 weeks of preconditioning at 2°C no runners occurred under either LD 10 h or 20 h, while runners were common in SD, particularly at 26°C and with 10 weeks of preconditioning (Rivero *et al.*, 2021 a).

Photoperiod enhanced the condition of *Fragaria* shoot cultures maintained at 4°C in SB strawberries (Reed, 2002). In SB strawberry cultivars 'Korona' and 'Elsanta', no cooling was required to re-establish normal leaf and inflorescence elongation and runner development under subsequent LD circumstances (Sønsteby and Heide, 2006).

4. Exogenous hormone

Gibberellins

Gibberellins are required for initiation of strawberry runners and inhibit GA production with PP333, AMO-1618, or prohexadione-calcium (Pro-Ca) (an inhibitor of the GA_3-oxidase enzyme) (Rademacher, 2000), causes the formation crown branches and reduces runner development (Avigdori-Avidov *et al.*, 1977; Nishizawa, 1993; Reekie and Hicklenton, 2002; Black, 2004; Hytönen *et al.*, 2009; Grez *et al.*, 2021). The GA20ox gene is mainly expressed in the axillary meristem dome and primordial, and in developing stolons. Runner less strawberries such as the woodland diploid strawberry (*F. vesca*) are caused by a mutation in the active site of a gibberellin 20-oxidase enzyme (GA20ox). As a result, GA3 stimulates runners development in all genotypes and species of strawberries, including the EB types of *F. vesca, F. virginiana*, and the EB and SB of *F. x ananassa* (Agafonov and Solovei, 1972; Solovei, 1972 a; Verzilov and Mikhteleva, 1974; Soetarto, 1979; Choma and Himelrick, 1984; Braun and Kender, 1985; Deyton *et al.*, 1991; Fouad *et al.*, 1991; Ra *et al.*, 1996; Dwivedi *et al.*, 1999 a, b; Paroussi *et al.*, 2002 a, b; Tenreira *et al.*, 2017; Li *et al.*, 2021 a; Godara *et al.*, 2022).

Overall, the effect of GA3 on runner growth was variable and dependent on GA concentration (Solovei, 1972 b; Mohammad *et al.*, 1990; Rajesh *et al.*, 2008), with GA3 at 50 ppm having no effect on runner growth in 'Sparkle' (SB) and 'Ozark Beauty' (EB) strawberries (Waithaka and Dana, 1978). According to Agafonov and Solovei (1974) GA3 administered to strawberries at a concentration of 0.005% improved the quantity of runners but decreased their quality. GA3 reduced runner growth at concentrations of 100 and 200 mg/L (Solovei, 1972 a). Application of 50 mg/L GA3 produced runner before flower in SD 'Camarosa' and 'Camroga' cultivars (Al-madhagi *et al.*, 2012). The number of strawberry 'Seolhyang' runners was reduced by GA3 foliar spray, which showed a negative correlation between the concentration and number of runners (Li *et al.*, 2020). Effect of GA3 on runner growth varies between cultivar (Solovei, 1972 a; Choma and Himelrick, 1984), with GA3 stimulating daughter-plant formation in the EB cultivar but suppressing it in the SB cultivar (Waithaka and Dana, 1978; Choma and Himelrick, 1984). According to Kender *et al.,* (1971) the response of three EB cultivars to GA3 at 50 increased runner development in cultivars 'Ozark Beauty' and 'Superfection', but had no effect on cultivar 'Geneva'.

Due to longer internodes, EB strawberry 'Tribute' and 'Selva' cultivars treated with GA3 produced fewer daughter plants (Dale *et al*., 1996). Compared to NAA and CCC, GA3 produced the greatest vegetative growth and runner production at 90 ppm on 'Sweet Charlie' (Rajesh *et al*., 2008). GA3 use was related to the frequency of applied (Tafazoli and Vince-Prue, 1978; Duarte and Hermosa, 1998). GAs increased runner production when applied prior to the onset of dormancy and during the chill requirement stage (Honda, 1972), but did not increase the number of runners and hastened flowering when applied about a month before the appearance of flower buds, while hastened fruit maturation when applied at the flowers opening stage.

Cytokinins

Exogenous benzyladenine (BA) resulted in a greater numbers of runners in certain studies (Kour *et al*., 2017; Liu *et al*., 2019), while cytokinin and auxin coordinate the dormancy and expansion of axillary buds in strawberries (Qiu *et al*., 2019).

The influence of the exogenous hormone cytokinin on vegetative development has also been studied by several researchers, BA-type cytokinin has been observed by several researchers to enhance runner induction (Waithaka *et al*., 1978; Waithaka and Dana, 1978; Kour *et al*., 2017; Liu *et al*., 2019). 6-BA also enhanced runner induction, with 50 mg/L being the most effective concentration (Li *et al*., 2020).

In 'Sparkle' (SB) and 'Ozark Beauty' (EB) strawberries, foliar spraying with PBA at 200-600 ppm increased runner production (Waithaka and Dana, 1978).

In contrast, BA alone had no effect on the generation of runners such as EB cultivar 'Geneva' (Kender *et al*., 1971), SB cultivars 'Pajaro', 'Queen Eliza', and 'Paros' (Momenpour *et al*., 2011) and 'Redchief' (SB) (Archbold and Strang, 1986). PBA caused axillary bud explants to grow into stolons (Waithaka *et al*., 1980).

Interaction of exogenous hormone on runner development

The effect of the combining hormones on strawberry runner development is based on a fight between them that prevents flowering. In EB 'Geneva' the use of both N6B and GA3 had a significant impact on runner formation (Kender *et al*., 1971). In 'Ozark Beauty' (EB), a combination of PBA and GA3 had a stronger impact on runners and daughter plant development than PBA alone, and PBA reduced rooting of daughter plants, which GA3 could not overcome (Waithaka and Dana, 1978). When BA and GA3 were combined, petioles and stolon internodes were less thickened and elongated, resulting in greater leaf area than when PBA was used alone (Waithaka and Dana, 1978).

The number of runners in the EB 'Tribute' and 'Selva' strawberries treated with GA3 and BA increased linearly when the benzyladenine (BA) concentration was increased up to 1800 mg/L, the recommend that BA at 1200 mg/L + GA3 at 300 mg/L in strawberries, under field or greenhouse conditions for runner formation (Dale *et al*., 1996). Application of 6-BA + ACC resulted in the maximum number of plantlets (six plantlets per plant) (Kirschbaum, 1998). In EB, GA3 at 50 ppm, BA at 50 ppm, or companion boosted the number of runners in 'Miyoshi' by 2-3 fold, whilst GA3 or GA3 + BA raised the number of runners by up to 8 and 4 times in 'Enrai' and 'Summer Berry', respectively (Pipattanawong *et al*., 1996).

Gibberellic acid, when combined with benzyladenine, significantly increased runner development in the Geneva cultivar, but benzyladenine alone had little impact (Kender *et al*., 1971).

Photoperiod × PGR

Day length photoperiod and gibberellin alone both increase runner production in strawberry cultivars with different genotypes and blooming habits. Strawberry plant susceptibility to exogenous gibberellins was enhanced by LD photoperiods (Tafazoli and Vince-Prue, 1978; Al-madhagi, 2012). The LD photoperiod increased the level of endogenous gibberellins, which promoted the growth of plant buds (Taylor *et al*., 1994). Meanwhile, the LD photoperiod had the same effect as gibberellin, leading to a greater number of epidermal cells, indicating that cell division and internodes length were increased (Nishizawa and Hori, 1993; Nishizawa, 1994). Suppression of GAs biosynthesis has been shown to promote crown branching, restrict runner production, and improve flowering by increasing the number of possible sites for floral induction and differentiation (Hytönen and Elomaa, 2011; Tenreira *et al*., 2017).

In a prolonged photoperiod, exogenous GA3 completely reversed the effect of prohexadione-calcium when transferring GA3-treated plants from short to long days, on the other hand, it restored normal runner development, this did not happen in plants that had not been treated with GA3 (Hytönen *et al*., 2009)

The influence of photoperiod and exogenous hormone interaction on the vegetative development of strawberries has been documented mainly with GA3. After exposure to the LD photoperiod, GA3 elicited comparable change in strawberries (Paroussi *et al.*, 2002 a).

The study by Soetarto (1979) discovered that during the 24 h photoperiod GA3 at 150 ppm improved the stolon length of cultivar 'Ostara'.

SD, DN, and LD photoperiods plus GA3 (50 ppm) resulting in the greatest vegetative growth in the LD photoperiod with 50 ppm GA3 application and greatest number of crowns/plant when plants in the LD photoperiod and treated with 1000 ppm CCC (Dwivedi *et al.*, 1999 a). Plants grow faster when treated with GA3 in the LD photoperiod than in the SD photoperiod (Paroussi *et al.*, 2002 a).

By increasing the level of soluble sugar in 'Seolhyang' the strawberry cultivar, LD photoperiod (16 h) and 50 mg/L 6-BA break the dormancy of axillary buds and produced runners (Li *et al*., 2020).

Gibberellins can compensate for the effects of environmental variables

However, chilled strawberry plants treated with GA3 in tropical countries (Kenya) produced about the same number of runners as those subjected to chilling alone, but plants treated with BA produced significantly more runners than chilling alone (Kahangi *et* *al*., 1992). When the plant was exposed to chilled conditions in conjunction with the treatment of BA + GA3, the number of runners increased (Kahangi *et al*., 1992). GA3 induced and enhanced vegetative growth, equivalent to the impact of four to six weeks of chilling (Tehranifar and Battey, 1997).

5. Discussion and Conclusions

The formation of strawberry runners was influenced by the interaction of genetic (cultivars), environmental (photoperiod, temperature, chilling hours or cold storage), and internal (hormones and carbohydrate) factors.

The most significant factor impacted by long-day photoperiod (LD) is the cultivar in strawberry runner proliferation. For the development of stolons in all flowering strawberry classes, LD and HT must interact. Additionally, in order for runners to grow in EB and SB strawberry cultivars, LD must surpass a certain value at HT (Darrow, 1937; Went, 1957; Smeets, 1980). This may have been connected to the influence of photoperiod on photosynthesis and the metabolism of carbohydrates, which suggested that the amount of carbohydrates may rise during the creation of runners and that the amount of soluble sugars was positively correlated with the number of runners (Li *et al*., 2020). Everbearing (EB) strawberries absorbed more CO_2 when temperature and irradiance rose (Rivero *et al*., 2021 b). However, the accumulation of photosynthates was not the only factor that affected the runner induction in cultivated strawberries (Li *et al.*, 2021 b). The photoperiod also enhanced the amount of endogenous hormone as well as the synthesis and accumulation of starch, sugar, amino acids, and protein (Li *et al.*, 2022). especially gibberellins that promote runner bud development (Taylor *et al*., 1994). And the effect of the application of gibberellins or photoperiod is the same result (Taylor *et al.*, 1994).

Meanwhile, more efficient runner production can be achieved in EB and SB strawberries by Gibberellins (GAs) Cytokinin and chilling period (CP) individually or in combination lead to production of stolons. In addition, CP or GAs enhances the effect of the photoperiod LD. Long cold storage or the chilling (CP) also works on converting starch to soluble sugars (López *et al*., 2002; Al-madhagi *et al*., 2018; Al-doubibi *et al*., 2021), and increased level of endogenous gibberellins (Avigdori-Avidov *et al*., 1977).

In fact, greater photosynthesis and respiration under the LD condition imply that more chemicals and energy are produced, which may account for the increased soluble sugar content in strawberry seedlings during runner production (Li *et al*., 2020). In which the respiration produced ATP and hydrolyzed the sugar for biosynthesis, resulting in altered levels and ratios of endogenous hormones, maybe with a focus on gibberellins and cytokinin, by transferring more sugar to axillary buds that are in high demand while restricting the quantity of sugar via the apical shoot (Mason *et al.*, 2014). In strawberry runners (non-dormant buds), as opposed to dormant buds, the expression of genes involved in sugar metabolism and signalling was also increased (Qiu *et al*., 2019). In order to explain the changes in signalling between stages of bud release to sustained development, Cao *et al.* (2023) propose a model of apical dominance that combines auxin, sucrose, strigolactones, gibberellins, and cytokinin.

The application of cytokinin helped to break the apical dominance and shift the auxin/cytokinin ratio (Al-madhagi, 2012; Qiu *et al.*, 2019), which led to the growth of axillary buds to runner (Li *et al*., 2020). This cytokinin appears to promote runnering in early development stage, but prolonged, elevated it levels inhibit runnering.

The application of AB-6 increased the level of free active of endogenous gibberellins and auxin in strawberry seedlings to a value higher than the free active of endogenous cytokinin (Al-madhagi, 2012) and increased the soluble sugar (Al-madhagi, 2012; Li *et al*., 2020). This ultimately converted polysaccharides into soluble sugars and stimulated axillary buds to produce runners. Additionally, the photoperiodic control the two genes (FvFT1) and (FvSOC1), that regulation of blooming and runners of woody strawberries (Hytönen and Kurokura, 2020). This may be able to explain how the interaction of photoperiod and temperature influences the growth of runners by enhancing photosynthesis, elevating endogenous hormone levels, raising respiration, and raising the amount of soluble sugars. In order to fully develop a runner in SB strawberries or partially generate in EB strawberries, the plant makes advantage of the indirect effects of photoperiod or cold storage as shown in figure 4.

It can be concluded that, in all strawberry cultivars (EB or SB), soluble sugars may be required for axillary buds to emerge from their dormant case and produce runners, when this is impacted by the applica-

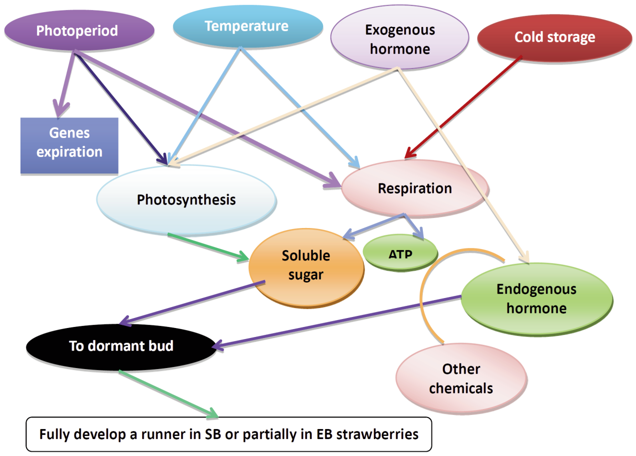

Fig. 4 - The effect of photoperiod, temperature, cold storage, and plant growth regulators alone or in combination prompted the plant to form runners by influencing the level of endogenous hormones and the level of sugar, whose level is raised in the axillary buds, prompting the plant to form runners.

tion of photoperiod LD or exogenous hormone.

The optimal strategy is determined by optimizing the planting date for propagation or changing the propagation conditions, depending on the cultivars and the seasonal environment (photoperiod × temperature) of the geographic region. Those factors are also important in the tissue culture technique as well as in the greenhouse or field.

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