agronomy

MDPI

Review

Factors Controlling Runner Formation in Strawberries

Yali Li [1,2], Byoung Ryong Jeong [3], Ping Huang [1], Xia Qiu [1], Feiyu Zhu [1], Jiaxian He [1], Liang Zhao [1], Si Wang [1], Xin Meng [4] and Mingzhong Ding [2,*]

[1] Institute of Remote Sensing and Digital Agriculture, Sichuan Academy of Agricultural Sciences, Chengdu 610066, China; liyali_irsa@scsaas.cn (Y.L.); huangping_irsa@scsaas.cn (P.H.); qiuxia_irsa@scsaas.cn (X.Q.); zhufeiyu_irsa@scsaas.cn (F.Z.); hejx1231@163.com (J.H.); zhao_liang@yeah.net (L.Z.); wangsi_irsa@scsaas.cn (S.W.)
[2] Sichuan Academy of Agricultural Sciences, Chengdu 610066, China
[3] Division of Horticultural Science, College of Agriculture and Life Sciences, Gyeongsang National University, Jinju 52828, Republic of Korea; brjeong@gmail.com
[4] Chengdu Agricultural Technology Extension Station, Chengdu 610042, China
* Correspondence: dingmingzhong_irsa@scsaas.cn

Abstract

Strawberry propagation relies predominantly on asexual reproduction via runner plants, making runners a critical organ for cultivation. Runners develop from axillary buds under specific environmental conditions. While long-day photoperiods and higher temperatures are key factors for inducing runner formation in most strawberry varieties, certain everbearing cultivars exhibit enhanced runner formation even under short-day conditions. Gibberellin (GA) is indispensable for runner bud outgrowth, with cytokinin and auxin synergistically regulating runner outgrowth. Genetically, GA biosynthesis genes strongly influence runner formation. Transcription factors such as LAM, SOC1, and HAN have recently been identified as key regulators. However, the genetic control of runner formation in strawberries, especially for cultivated octoploid strawberry cultivars, is not yet fully elucidated. This review synthesizes current knowledge on the environmental and genetic regulation of strawberry runner induction, providing a theoretical foundation for artificial control of runner formation.

Keywords: auxin; axillary bud; cytokinin; gibberellin; light conditions; tissue sugar level; temperature

Academic Editor: Francis Drummond

Received: 6 August 2025
Revised: 8 September 2025
Accepted: 20 September 2025
Published: 22 September 2025

Citation: Li, Y.; Jeong, B.R.; Huang, P.; Qiu, X.; Zhu, F.; He, J.; Zhao, L.; Wang, S.; Meng, X.; Ding, M. Factors Controlling Runner Formation in Strawberries. *Agronomy* **2025**, *15*, 2235. https://doi.org/10.3390/agronomy15092235

1. Introduction

Stolons are stems that grow horizontally along the ground surface. They consist of two elongated internodes with a dormant bud at the middle node. A daughter plant and the next stolon segment develop from the second node. This linear growth pattern results in daughter plants spaced along the stolon, creating the appearance that they are "running away" from the mother plant. Hence, stolons are also called runners [1]. Runners are important organs for asexual reproduction in plants; indeed, many species propagate using the daughter plants (transplants) produced on runners, including strawberry (*Fragaria* spp.) [2], potato (*Solanum demissum*) [3], white clover (*Trifolium repens*) [4], bermudagrass (*Cynodon dactylon*) [5], and licorice (*Glycyrrhiza glabra*) [6].

Strawberry is an herbaceous perennial crop in the Rosaceae family. It is one of the most popular fruit crops around the world for its beautiful appearance, flavor, and health benefits. In 2023, global strawberry cultivation covered 591,295 hectares, with a yield of 14,700,937 tons (FAOSTAT, https://www.fao.org/faostat/en/#data, accessed on 22 March 2025). As a result

of this popularity, both cultivation area and production continue to increase steadily, driving extremely high demand for strawberry transplants. Consequently, strawberry propagation has attracted significant research interest. Strawberries can be propagated either sexually via seeds or asexually via runner plants [7–9]. Asexual propagation is typically preferred because seed germination rates are very low [10] and because cultivated strawberries are highly heterozygous, leading to character separation in seed-propagated offspring [11]. Therefore, commercial production relies on runner propagation to maintain clonal fidelity and desired maternal traits [12]. It should be noted that the number of runners produced by strawberries varies by cultivar [13–18], typically yielding fewer than 50 daughter plants per mother plant annually. This limitation necessitates substantial land resources for transplant production. Thus, understanding the regulatory mechanisms of runner formation is critical for efficiently producing high-quality transplants within limited land areas.

The strawberry plant features a highly compressed main stem (primary crown) with short internodes [19]. Each node bears a single trifoliate leaf and an axillary bud (AXB) at the petiole–stem junction (Figure 1). The AXBs at the axils of leaves may remain dormant or develop new shoots. There are two kinds of axillary shoots in strawberry plants: runners and branch crowns (flowering shoot) [20]. AXB fate determination shapes plant architecture and occurs through two developmental phases: initiation and subsequent outgrowth [21]. However, AXB initiation remains incompletely understood, particularly in rosaceous crops [22]. Nevertheless, it is clear that AXB initiation and outgrowth are regulated temporally and spatially [23]. Generally, the outgrowth of the AXB depends on its location on the primary crown, with the uppermost AXB having the highest priority for development into a runner or a branch crown [24]. Furthermore, evidence from both wild and cultivated strawberries indicates that the development of AXBs into either runners or branch crowns is a genetically distinct and mutually exclusive process. The predominance of one developmental pathway over the other is intricately regulated by genetic and environmental factors [25]. In light of this, this review analyzes these regulatory mechanisms to advance understanding of runner formation in strawberry.

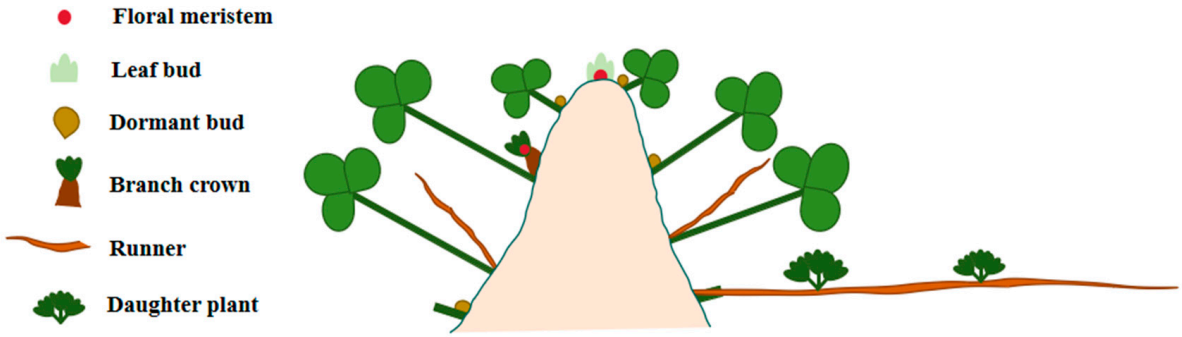

Figure 1. A diagram of the primary crown of a strawberry plant. The primary shoot is composed of leaves, with axillary meristem at each axils of leaves and is terminated by a floral meristem. Along the primary crown, the axillary meristem can develop into either branch crowns or runners or stay dormant. Daughter plants are new plants that grow on runners.

2. Environmental Control of Runner Formation

2.1. Light

2.1.1. Photoperiod

Strawberries can be broadly categorized into two types based on their photoperiodic response: seasonal flowering strawberries, which are also called June-bearing or once-season flowering plants, and everbearing strawberries, also referred to as perpetual flowering, remontant, repeat flowering, or day-neutral plants in different reports [26–28].

In strawberries, runner development is closely associated with flowering. In most cases, even the same environmental signal may elicit contrasting effects on runner formation and flowering. For example, seasonal flowering strawberries produce runners during longer days (LD), which is why these strawberries are usually propagated in summer (Table 1). Researchers have found that when seasonal flowering strawberry plants were transferred from LD to short-day (SD) conditions, the development of new runners ceased after nine weeks. Similarly, when strawberry plants were exposed to SD conditions for the same brief period, runner formation was reset when the plants were re-exposed to LD conditions [29]. Moreover, LD was also found to inhibit flowering and induce runner formation in wild-type seasonal flowering strawberries (*Fragaria vesca*) [30,31]. Previous research proved that photoperiods between 16 h and 22 h were beneficial for runner formation in the strawberry cultivars 'Sulhyang' and 'Maehyang', and the number of runners induced was positively correlated with the duration of photoperiod [32]. In contrast, as everbearing genotypes are characterized by persistent flowering and fruiting, they are responsible for poor runner formation compared with seasonal flowering genotypes [33]. Interestingly, runner formation was enhanced by SD over the same intermediate-to-high temperature range in some everbearing cultivars, such as Hawaii-4 [25,34]. Moreover, some everbearing strawberry cultivars did not show any significant differences in runner induction under LD and SD conditions [35]. Thus, the effect of photoperiod on runner induction in everbearing strawberries is much more complicated.

2.1.2. Light Intensity

High light intensity generally promotes runner formation and daughter plant growth. Specifically, more runners were produced by mother plants when provided with suitable high light intensity during the day, and increasing the light intensity of supplemental light for extending the photoperiod also promoted the number of runners produced in air-conditioned glasshouses [36]. In a closed transplant production system using fluorescent light, the strawberry cultivar 'Albion' produced more daughter plants under 280 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD) than under 140 or 220 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD, which resulted in a daily productivity of about 0.27 daughter plants per plant, and the growth of daughter plants was improved by increasing the light intensity during strawberry propagation [37]. Similarly, Wu et al. compared the effects of different light intensities on daughter plant propagation of the 'Toyonoka' strawberry cultivar under fluorescent light and found that high light intensity (110–122 $\mu mol \cdot m^{-2} \cdot s^{-1}$) promoted runner formation and daughter plant growth compared with lower light intensity (50–55 $\mu mol \cdot m^{-2} \cdot s^{-1}$) [38]. Recent research has found that the number of runners and runner plants produced by 'Benihoppe' mother plants increased by 38.9% and 33.7%, respectively, when the daily light integral increased from 8.6 to 11.5 $mol \cdot m^{-2} \cdot d^{-1}$; it should be noted that the optimal daily light integral for the propagation of this strawberry cultivar ranges from 11.5 to 17.3 $mol \cdot m^{-2} \cdot d^{-1}$ [39]. Furthermore, increasing the light intensity received by mother plants rather than that received by runner plants was more effective in enhancing the growth of runner plants [40]. Thus, the efficiency of strawberry propagation in a controlled environment condition may be improved by increasing only the light intensity received by mother plants.

2.1.3. Light Quality

The light quality supplied to strawberry directly influences photosynthesis [41], which is tightly correlated with runner formation. Studies have indicated that blue and far-red spectra of light delayed flowering and stimulated runner development [42,43]. Additionally, recent research has also shown that interrupting supplemental night blue light at

20 μmol·m^{-2}·s^{-1} PPFD for 4 h under SD conditions significantly increased the number of runners and daughter plants [44], indicating that low-intensity blue light has the ability to stimulate AXBs to develop into runners. Moreover, different qualities of high-intensity night interruption light (70 μmol·m^{-2}·s^{-1} PPFD), including blue, red, green, white, and far-red spectra of light, significantly increased the number of runners and daughter plants induced per plant compared with those exposed to SD conditions; furthermore, among these spectra of light, red light seems to play a better role in the vegetative growth of strawberry runner plants compared with other light spectra [32]. Thus, a big percentage of red light was used for strawberry propagation; for instance, a combination of 30% blue and 70% red light by PPFD induced the greatest number of runners and daughter plants per mother plant for the strawberry cultivar 'Toyonoka' [38].

2.2. Temperature

Besides light, temperature is another crucial environmental factor. Higher temperature is critical for runner induction in different types of strawberries, and high-temperature-induced runner formation is independent of photoperiod to some extent [45], except for some runnerless everbearing genotypes of *Fragaria vesca* (woodland strawberry) [30]. In most cases, air temperatures above 18 °C stimulate runner formation, while the ideal temperature for runner induction varies by strawberry cultivars [46].

Recent research showed that chilling (0–5 °C) and cold (below 0 °C) storage increased runner production in both seasonal flowering and everbearing strawberries [47]. Specifically, runner induction was promoted when the chilling period was more than 1000 h in several everbearing cultivars [48,49]. Similarly, longer cold storage also improved runner production in several seasonal flowering strawberry cultivars [50,51]. Recently, research has also found an interaction between the length of cold storage and the LD photoperiod for runner formation [34,52]. For instance, strawberry exposure to prolonged photoperiods and longer cold storage duration improves runner production, especially in several everbearing cultivars [48]. However, chilling and cold storage are not used for runner induction, because this kind of low temperature may decrease the quality and quantity of daughter plants [53].

Table 1. Effect of light conditions and temperature on runner formation in strawberry plants.

No.	Variety	Cultivar	Light Condition	Temperature	Optimal Treatment	Reference
1	*Fragaria* × *ananassa* June-bearing	Seolhyang	8, 12, or 16 h photoperiod at 300 μmol· m^{-2}· s^{-1} PPFD	27/13 °C, 25/15 °C, or 23/17 °C (day/night)	16 h + 25/15 °C	[54]
2	*Fragaria* × *ananassa* June-bearing	Sulhyang, Maehyang	Photoperiod from 12 to 22 h with 250 μmol·m^{-2} ·s^{-1} PPFD; 4 h NI light provided by red, blue, green, white, or far-red LED light	25/15 °C (day/night)	20 h photoperiod and red LED light	[32]
3	*Fragaria* × *ananassa* Everbearing	Natsuakari, Dekoruju'	Natural day length or 16 h photoperiod	0, 700, 1000, 1500 and 2000 h of chilling (<5 °C)	More than 1000 h chilling	[52]
4	*Fragaria* × *ananassa* June-bearing	Tochiotome	Plants grown under 10 h SD in a glasshouse for 0, 14 or 28 d, then under 13 h LD for 49, 35 and 21 d, respectively,	23/17 °C (day/night)	13 h LD for 49 d	[55]
5	*Fragaria* × *ananassa* June-bearing	Toyonoka	100% red light, 70% red light + 30% blue light, 70% red light + 20% blue light + 10% green light	25/20 °C (day/night)	70% red light + 30% blue light	[38]
6	*Fragaria* × *ananassa*	Saga, Sonata, Nobel, Florence, Rumba, Malwina	10 h SD or 20 h LD	9, 15, 21, or 27 °C	Temperature over 21 °C in SD and over 15 °C in LD	[56]
7	*Fragaria* × *ananassa* June-bearing	Akihime	White LEDs, white and red LEDs, red and blue LEDs, and red, blue and green LEDs	25/20 °C (day/night)	White LEDs	[57]

Table 1. *Cont.*

No.	Variety	Cultivar	Light Condition	Temperature	Optimal Treatment	Reference
8	F1-Hybrid, Everbearing	Delizzimo	10 h SD or 20 h LD	12, 19, or 26 °C	10 h SD + 26 °C	[34,58]
9	*Fragaria vesca*	Original cultivars in Norwegian	10 h SD or 24 h LD	9, 15, or 21 °C	24 h LD + 21 °C	[45]
10	*Fragaria* × *ananassa*	Earliglow, Seneca, Jewel, Chandler Cavendish	Preforcing 8 h SD for 0, 1, 2, 4 weeks, then transfer to 16 h LD	Preforcing at 15 °C for 0, 1, 2, 4 weeks, then transfer to 20 °C	Chandler: preforcing at 15 °C + 8 h for 4 weeks; other cultivars: no preforcing treatment	[59]
11	*Fragaria* × *ananassa* Everbearing	Albion	10 h SD, 18 h and 24 h LD; far-red: blue (1:5, 5:1 and 1:1)	Nature temperature for photoperiod expt.; 24 °C/18 °C (day/night) for light quality expt.	Very few runners produced, and no significant difference in runner production between photoperiods and light qualities	[60]
12	*Fragaria* × *ananassa* Everbearing	Capri	2 or 4 weeks NI light for 30 min·h^{-1} at 10 W·m^{-2}	Nature temperature	No NI treatment	[61]
13	*Fragaria* × *ananassa*	Honeoye (SD), Tribute (day-neutral), RH 30 (day-neutral)	9 h SD or 16 h LD	14, 17, 20, 23, 26, or 29 °C	Honeoye: 26 °C + 16 h LD; RH30: 26 and 29 °C + 16 h LD; Tribute: 23 °C + 16 h LD	[62]
14	*Fragaria* × *ananassa* Everbearing	Favori	10 h SD or 20 h LD	6, 16 or 26 °C for 5 and 10 weeks	21 °C + 20 h preconditioning for 10 weeks	[34]

Note: NI, night interruption; SD, short day; LD, long day.

2.3. Inorganic Nutrients

Nutrient management is fundamental to strawberry development, as strawberries are highly sensitive to fertilizers, particularly those grown in hydroponic systems. Researchers found that macroelements, including nitrogen (N), phosphorus (P), and potassium (K), are crucial for runner formation. In the strawberry 'Enrai', applying N, P_2O_5, and K_2O (15-15-15) at 100 mg per pot yielded the greatest number of runners compared with 0 mg or 50 mg per pot [63]. Recent studies further confirm that N is the most critical nutrient for runner production, as runner numbers under N deficiency were significantly lower than under deficiencies of other elements [64]. Among microelements, zinc-treated strawberries produced more runners than iron-treated plants, with the highest runner count observed in plants treated with 0.4% $FeSO_4$ combined with 0.4% $ZnSO_4$ [65]. This enhancement may be attributed to zinc's beneficial role in stimulating meristematic activity [66].

2.4. Regulation Network Behind Environment

The antagonism between runner formation and flowering represents a classic example of developmental trade-offs in plants, fundamentally driven by the competition for limited resources [67]. This trade-off is strategically managed through a centralized genetic regulatory network that interprets environmental cues to direct energy allocation towards either vegetative propagation (runners) or sexual reproduction (flowers and fruits). From an evolutionary perspective, this plasticity in developmental fate allows strawberry species to adapt to diverse and fluctuating environments [25]. In favorable conditions with long days and warm temperatures (typically indicative of a long growing season), the plant invests in vegetative expansion via runners to colonize space and generate new clonal individuals. Conversely, the onset of short days and cooler temperatures (often signaling the end of the growing season) triggers a shift towards reproductive investment, ensuring seed set and genetic diversity before senescence. The complex interplay observed in everbearing genotypes, which balance both processes, may reflect an adaptive strategy to exploit unpredictable or extended growing periods.

At the molecular level, this trade-off is orchestrated by a key genetic pathway. Figure 2 integrates environmental control of both processes in seasonal flowering strawberries. Under LD conditions, the CONSTANS (CO) homolog activates *FLOWERING LOCUS T1* (*FT1*) in leaves, leading to upregulation of *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*) in the shoot apex [31,67,68]. Subsequently, *SOC1* upregulates *TERMINAL FLOWER1* (*TFL1*), which inhibits flowering by downregulating key floral genes *FT3* and *APETALA1* (*AP1*), while promoting runner formation. Regarding light quality,

blue, red, and far-red light regulate runner formation by affecting *CO* and *CONSTITUTIVE PHOTOMORPHOGENIC 1* (*COP1*) expression. COP1 mediates CO degradation, reducing its abundance. Blue and far-red light suppress this degradation via cryptochrome 2 (cry2) and phytochrome A (phyA), respectively. Red light entrains a circadian oscillator driving *CO* transcription but also destabilizes CO protein through phyB to maintain the level of CO [69]. Temperature primarily regulates runner formation through *TFL1* expression: high temperature promotes it, while low temperature suppresses it indirectly [70,71], though the exact pathway remains unknown. Additionally, the reduced runner phenotype in everbearing strawberries results from a TFL1 frameshift mutation that produces a non-functional protein incapable of promoting runner formation even under LD and high-temperature conditions [72].

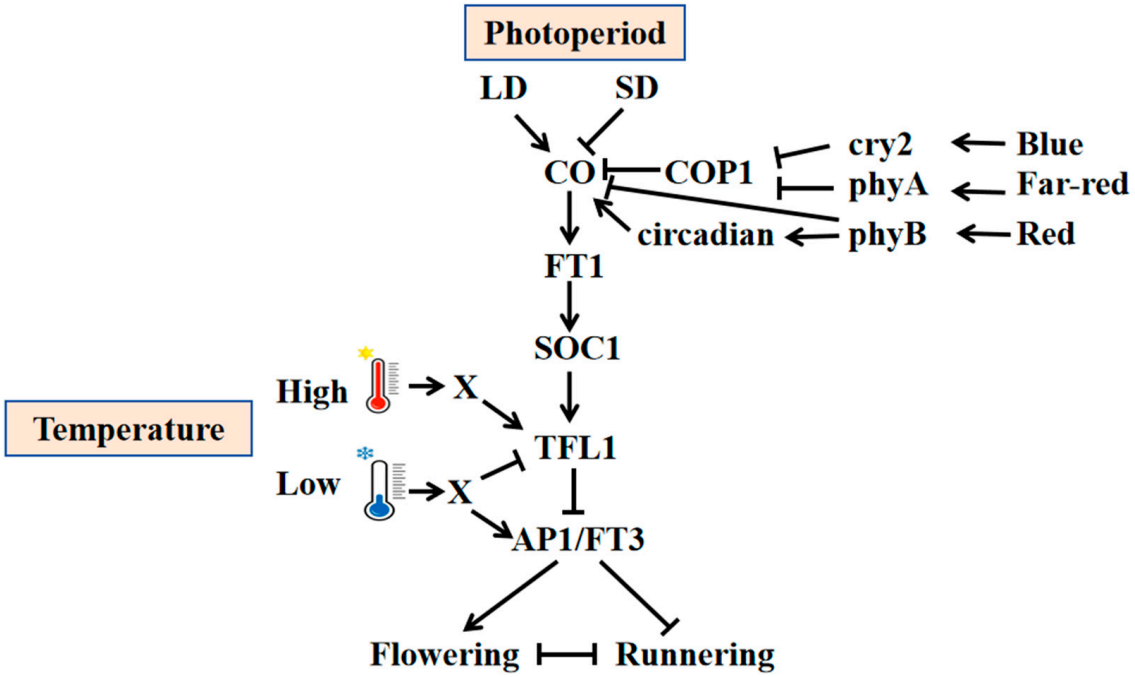

Figure 2. Current model for controlling runner formation by light and temperature in seasonal strawberries. Arrows indicate activation, while bars indicate repression, and "X" means unidentified regulators. The gene encoding strong floral repressor TFL1, which promotes runner formation, is regulated by ambient temperature through unknown mechanisms. And TFL1 is also regulated by photoperiodic signals (LD and SD) mediated by CO via FT1 and SOC1. Blue, red, and far-red light also affect runner formation through CO.

3. Hormonal Control of Runner Formation

3.1. Gibberellic Acids (GAs)

GAs significantly increased the number of runners in both wild and cultivated strawberries [73–75], whereas prohexadione-calcium, a GA biosynthesis inhibitor, suppresses runner formation [30,76,77]. The crucial role of GAs in runner formation was later genetically validated. Tenreira et al. identified a 9-bp deletion in the active site of *FveGA20ox* (a GA biosynthesis gene), causing runnerless phenotypes in woodland strawberry [20]. This mutation occurs in all natural runnerless woodland strawberries, and exogenous application of bioactive GA restores runner production in these plants. In contrast, some studies report that exogenous GA_3 reduces runner numbers in cultivated strawberries (Table 2) [78,79]. This suggests GA concentrations must remain within an optimal range for runner formation, as both excessive and insufficient levels inhibit the process. This discrepancy may be explained by the fact that cultivated strawberries are com-

plex allo-octoploids, and polyploid plants typically produce higher hormone levels than diploid counterparts [80,81]. Consequently, nearly all cultivated strawberries can produce runners, but exogenous GA_3 may disrupt this hormonal equilibrium, thereby reducing runner numbers.

3.2. Cytokinins and Auxins

Cytokinin and auxin coordinate the regulation of dormancy and outgrowth of axillary buds (AXBs) in strawberries [82]. Cytokinins are primarily synthesized in roots and exported, while auxin is mainly produced in terminal buds and transported basipetally [83]. A high cytokinin-to-auxin ratio in AXBs triggers bud growth. Studies reveal elevated auxin activity in dormant buds versus high cytokinin activity in non-dormant buds. Decapitation and pharmacological experiments demonstrate that both reduced auxin accumulation and exogenous cytokinin application initiate bud growth [82]. However, whether the AXBs will develop into branch crowns or runners after cytokinine application is uncertain. It may be determined simultaneously by the environment in which the plants live. For instance, benzyl adenine (BA) and thidiazuron (TDZ) are the most commonly used cytokinin for runner induction in strawberries (Table 2) [14,84]. Researchers found that application of BA at 50 $mg \cdot L^{-1}$ increased runner formation in strawberries under a condition of LD and moderate temperatures [84–86], while exogenous applications of TDZ induced more branch crowns than runners during winter time when the temperature was low with SD condition [87], These results indicate cytokinins combined with high temperature and/or LD conditions promote runner development from AXBs.

3.3. Other Plant Growth Regulators

Plant growth regulators like strigolactones (SLs) and abscisic acid (ABA) also regulate runner formation. Similar to auxin, SLs effectively inhibit branching [88]. Research shows auxin moves basipetally along stems, suppressing AXB (axillary bud) outgrowth and branch crown development partly by promoting SL biosynthesis [89,90]. Recent studies demonstrate that spraying the SL analog rac-GR24 on strawberry crowns inhibits runner sprouting (Table 2) [91]. This suppression likely occurs via inhibition of cytokinin signaling and enhancement of ABA pathways (Figure 3). Early research confirmed that exogenous ABA inhibits runner formation in strawberries [92]. ABA was proposed to be a general inhibitor of AXB outgrowth [93]. This action is often BRANCHED1 (BRC1) dependent on multiple species [94,95]. Among these species, ABA is induced by the transcriptional regulator BRC1, which is expressed in AXBs and axillary branches and then prevents bud outgrowth [96].

Table 2. Effect of hormones on runner formation in strawberry plants.

No.	Cultivar	Hormone	Concentration	Runner Development	Reference
1	Pajaro, Queen Eliza, Paros	GA and BA	300 and 1200 ppm, respectively	Inhibited runner production	[14]
2	Seolhyang	BA and IBA	50 $mg \cdot L^{-1}$	Increased runner production	[87]
3	Seolhyang	TDZ	50 $mg \cdot L^{-1}$	Increased runner production	[87]
4	Seolhyang	TDZ and IBA	50 $mg \cdot L^{-1}$	Increased runner production	[87]
5	Seolhyang	TDZ and IAA	50 $mg \cdot L^{-1}$	Increased runner production	[87]
6	Korona	GA_3	5000 $mg \cdot L^{-1}$	Increased runner production	[30]
7	Ruegen	GA_3	50, 75, 100 $mg \cdot L^{-1}$	Increased runner production	[97]
8	Maehyang	6-BA	900 or 1500 $mg \cdot L^{-1}$	Increased runner production	[98]
9	Maehyang, Sulhyang	BA	100 $mg \cdot L^{-1}$	Increased runner production	[86]
10	Maehyang, Sulhyang	Chlormequat chloride	100 $mg \cdot L^{-1}$	No effect	[86]
11	Cardinal	Paclobutrazol	75, 150, 300, 600, or 1200 $mg \cdot L^{-1}$	Inhibited runner production	[99]
12	Benihoppe	Strigolactones	5, 10, or 20 $\mu mol \cdot L^{-1}$	Inhibited runner production	[91]
13	Superfection	ABA	50 ppm	Inhibited runner production	[92]

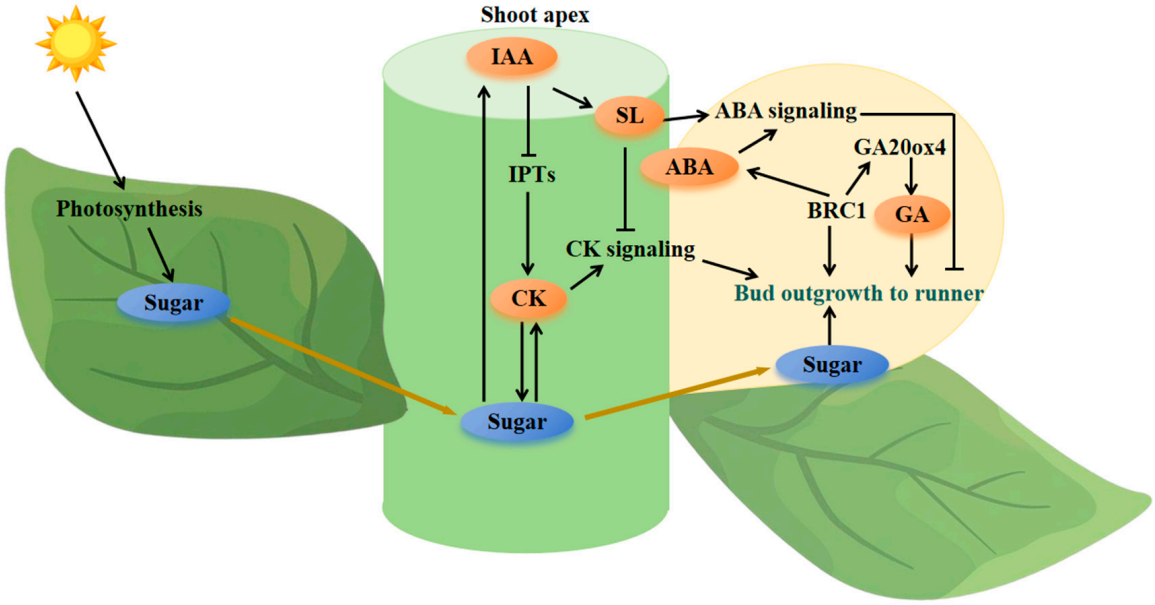

Figure 3. The putative mechanism diagram for strawberry runner formation affected by hormones and sugar. Arrows indicate activation, and bars indicate repression. CK: cytokinin; IAA: indole-3-acetic acid; SL: strigolactones; ABA: abscisic acid; GA: gibberellin. *IPTs*: isopentenyltransferase, key gene for cytokinin synthesis; *GA20ox4*: key gene for gibberellin synthesis; *BRC1*: *BRANCHED1*, key hub gene that is involved in the control of branching.

3.4. Sugar

Sugar content positively correlates with the number of runners and daughter plants [80], indicating the essential role of sugars in strawberry runner formation. Research demonstrates that glucose is a key sugar regulating this process [91,100]. AXB outgrowth is controlled by sugar metabolic and signaling pathways in multiple species, including rose (*Rosa hybrida* L.) [101], grasses [102], and *Chrysanthemum Morifolium* [103]. This process consistently interacts with hormonal signaling networks [104]. For instance, sucrose induced AXB outgrowth via the auxin transport pathway in chrysanthemum [103]. Another study suggests that sugar-mediated suppression of auxin-induced strigolactone pathways promotes bud outgrowth independent of cytokinin in rose and pea [105]. However, sucrose promoted AXB outgrowth through enhancing the accumulation of cytokinin in potato (*Solanum tuberosum*) [106]. These findings reveal complex sugar–hormone signaling networks likely regulating strawberry runner formation, warranting further investigation.

4. Genetic Control of Runner Formation

Fragaria species are classified by ploidy levels ranging from diploid (2×) to decaploid (10×). Most cultivated strawberries are octoploid (*Fragaria* × *ananassa*), originating from hybridization between the octoploid subspecies *F. chiloensis* and *F. virginiana* [107]. Cytological and genomic studies indicate that at least two diploid progenitors from the Fragaria species (*F. vesca* and *F. iinumae*) contributed to the octoploid genomes of both *F. virginiana* and *F. chiloensis*. Within *F. ananassa*, the *F. vesca*-derived subgenome demonstrates higher gene retention and expression dominance, establishing it as the primary genomic contributor [108]. Consequently, *F. vesca* serves as an emerging model system for studying runner development [26,109,110]. Nevertheless, research indicates that the genetic regulation of runner formation differs somewhat between woodland and cultivated strawberries.

4.1. Runner Formation in Woodland Strawberry

The diploid woodland strawberry has different natural accessions with or without runners. For instance, 'Yellow Wonder', 'Alpine', and 'Ruegen' do not develop runners [111–113], whereas 'Hawaii 4', 'Snovit', and 'Norrlandssmultron' produce runners [114,115]. The difference in runner formation between runner-forming and runnerless strawberries was first found to be caused by a natural mutation in the GA biosynthesis gene *FveGA20ox4* [20]. Meanwhile, the GA signal suppressor gene *FveRGA1* negatively regulates runner formation in diploid woodland strawberry [116,117]. The studies that served as the basis for the illustration in Figure 4 highlight the important role of GA in runner formation in strawberries. However, GA primarily promotes AXB outgrowth rather than bud initiation [118]. A gene named *Loss of Axillary Meristems* (*LAM*) has recently been found to act sequentially with GA from bud initiation to runner outgrowth in woodland strawberry. Genetic studies indicated that lam is epistatic to *suppressor of runnerless* (*srl*, a mutant of *FveRGA1*) during runner formation. As LAM and *FveRGA1* play sequential roles in runner formation, they may not interact directly with each other [21]. Moreover, *LAM* encodes a GRAS transcription factor in the *LATERAL SUPPRESSOR* (*LAS*) subfamily, which is a hub gene in the gene regulatory network [119]. In *Arabidopsis*, *LAS* directly interacts with the GA pathway and binds to the promoter of a GA deactivation enzyme *GA2ox4*, leading to a low-GA content region in the leaf axil [118]. Thus, it can be speculated that a low level of GA is required during bud initiation in strawberry, a phenomenon identified in grapevine [120]. The *CUP-SHAPED COTYLEDON2* (*CUC2*) directly binds to the promoter of *LAS* in *Arabidopsis* [121]. Since the fvecuc2a mutant has a phenotype similar to that of the lam mutant in *F. vesca* [21,122], *CUC* may also be an upstream gene of *LAM* in *F. vesca*. By referring to the initiation and outgrowth of axillary buds in other plants [123], Figure 4 proposes a *hypothetical* model for runner formation control in woodland strawberry. The expression level of gene *SHOOTMERISTEMLESS* (*STM*) reflects axillary meristem activity. *STM* is regulated by *CUC* genes and additionally modulated by *LAS* via *REVOLUTA* (*REV*). Following meristem activation, cytokinins promote increased *WUSCHEL* (*WUS*) expression to initiate meristem development. *WUS* then directly activates the stem cell marker *CLAVATA3* (*CLV3*), establishing the axillary meristem. Notably, this developmental model requires further experimental validation.

4.2. Runner Formation in Cultivated Strawberry

The genetic control of runner formation in cultivated strawberries is highly complex due to the large number of chromosomes (2n = 8X = 56). Several studies indicate runner production follows quantitative inheritance governed by numerous quantitative trait loci (QTLs). Gaston et al. [7,124] found that a single major QTL named *Perpetual Flowering and Runnering* (*FaPFRU*) negatively regulates runner formation in cultivated perpetual flowering strawberries, and *FaPFRU* was further identified in a 2.85 Mb region on chromosome 4A in all subgenomes belonging to chromosome 4 [125]. Interestingly, QTLs on the diploid chromosome 4 were also associated with the number of runners in *F. vesca*, with an overlapping QTL in chromosome 4 for flowering time [108], indicating this QTL on chromosome 4 may be the same QTL as *PFRU* in cultivated strawberry. Recently, new DNA markers were developed to narrow the *PFRU* candidate region [126]. In contrast, Hossain et al. [33] identified seven QTLs, named qRU-5D, qRU-3D1, qRU-1D2, qRU-4D, qRU-4C, qRU-5C and qRU-2D2, responsible for runner formation in octoploid strawberries. These QTLs were not orthologous to *FaPFRU*, suggesting that the genetic control of runner formation in octoploid strawberries is complex.

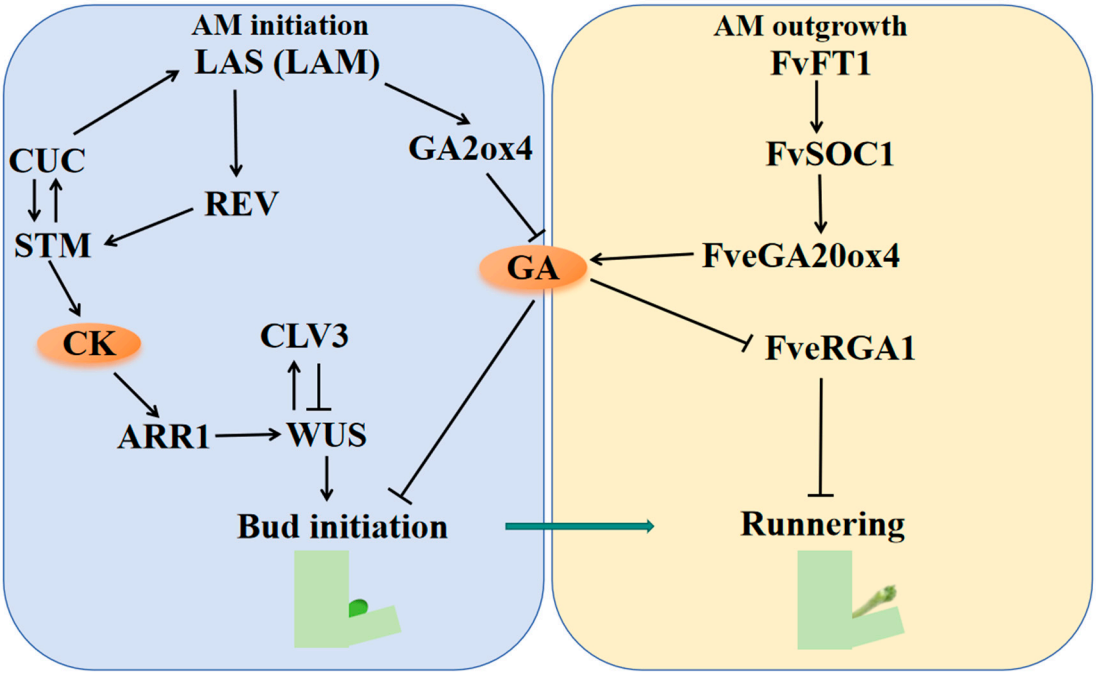

Figure 4. Hypothetical model of runner formation in woodland strawberry. Arrows indicate activation, and bars indicate repression. Gibberellin (GA) significantly promotes axillary meristem (AM) outgrowth but may inhibit AM initiation. CK: cytokinin; LAS: LATERAL SUPPRESSOR; LAM: Loss of Axillary Meristems; REV: REVOLUTA; CUC: CUP-SHAPED-COTYLRDON; STM: SHOOT MERISTEMLESS; ARR1: Arabidopsis response regulator1; WUS:WUSCHEL; CLV3: CLAVATA3; FT1: FLOWERING LOCUS T1; SOC1: SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1.

A recent study revealed that the gene *HANABA TARANU* (*FaHAN*) encodes a GATA transcription factor that increases the number of runners in cultivated strawberry [127]. It also suppresses the expression of *BRC1*, which plays a key role in inhibiting AXB outgrowth. Furthermore, it influences the expression level of the master regulator of the meristematic identity gene *FaSTM*. *FaHAN* also activates several genes involved in GA biosynthesis and cytokinin signaling pathways to promote runner outgrowth. Further assays indicated that *FaHAN* could be directly activated by FaNAC2, revealing a FaNAC2-FaHAN pathway in the control of AXB initiation and outgrowth for runner formation in cultivated strawberry. Nevertheless, a great deal of work is still needed to reveal the genetic mechanism underlying runner formation in strawberries.

5. An Integrated Conceptual Framework for Runner Formation

The complex regulation of strawberry runner formation involves a multi-layered network in which environmental signals, hormonal pathways, and genetic programs interact synergistically. When strawberry plants are exposed to environmental stimuli, such as LD conditions, high light intensity, red and blue light spectra, and elevated temperatures, they are transduced into developmental responses through a core genetic module, comprising CO-FT1-SOC1, which acts as a major integrator. The key downstream regulatory node is *TFL1*, whose expression is promoted by SOC1 under inductive conditions. In diploid strawberries, GA levels increase through the elevated expression of biosynthesis gene *FveGA20ox4*, which is stimulated by SOC1, thereby promoting runner formation. In octoploid strawberries, the GATA transcription factor FaHAN serves as a critical positive regulator, likely acting upstream by repressing the branching inhibitor BRC1 and activating genes involved in GA and cytokinin pathways. Additionally, cytokinin facilitates bud release from dormancy, whereas auxin, SLs, and ABA suppress runner for-

mation. Sugar availability provides essential metabolic energy and signaling input that interact closely with hormonal pathways to facilitate runner formation. This integrated framework underscores that runner formation is not a linear pathway but a complex web of interactions.

6. Future Prospects

Although the influence of environmental cues and hormonal regulators on strawberry runner formation has been studied for decades, the practical application of these findings remains limited. Fortunately, the convergence of this knowledge with artificial intelligence now offers transformative potential. By integrating historical and real-time phenotypic data with environmental/hormonal parameters, AI-powered developmental prediction models can forecast runner initiation dynamics and optimize propagation timelines. These systems enable intelligent decision-making, including automatically adjusting light regimes, nutrient solutions, or hormone treatments based on predicted developmental stages and propagation targets. Indeed, there have been some studies on the formation of strawberry runners in smart plant factories, and most of these studies have focused on LED lights [128,129]. Further refinement of the optimal photoperiod, light intensity, and light quality ratios for the formation of runners in different strawberry varieties will help AI to more accurately regulate the formation of strawberry runners. This AI-driven approach addresses labor shortages and aligns with smart agriculture trends, mitigating propagation risks while maximizing efficiency and yield consistency in strawberry nurseries.

Despite progress, the core molecular mechanisms orchestrating strawberry runner formation remain largely elusive, particularly the specific signaling pathways, gene regulatory networks, and cell-type-specific events driving axillary bud fate determination towards runners. Unraveling this complexity is a fundamental challenge. However, the emergence of advanced single-cell and spatial omics technologies presents a transformative opportunity. For instance, Roszak et al. deeply characterized the developmental trajectory of Arabidopsis protophloem, which occurs in as few as 19 cells [130]. Applying these techniques to strawberry crown and axillary meristem tissues can delineate the distinct molecular profiles of cell populations involved in runner initiation and outgrowth under varying conditions. This cell-resolution approach offers a powerful new strategy to pinpoint key regulatory genes, hormone signaling hubs, and cellular interactions critical for runner formation, thereby providing unprecedented mechanistic insights and novel targets for molecular breeding or biotechnological intervention.

Author Contributions: Conceptualization, Y.L. and B.R.J.; validation, P.H. and S.W.; formal analysis, L.Z.; resources, M.D.; data curation, X.Q. and J.H.; writing—original draft preparation, Y.L.; writing—review and editing, B.R.J., S.W., and M.D.; visualization, F.Z.; supervision, P.H.; project administration, X.M.; funding acquisition, P.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (no. 32402488), the Sichuan Science and Technology Program (2024NSFSC1453), and the Science and Technology Program of Sichuan Academy of Agricultural Sciences (5+1QYGG006/2022ZZCX032).

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Guo, L.; Plunkert, M.; Luo, X.; Liu, Z. Developmental regulation of stolon and rhizome. *Curr. Opin. Plant Biol.* **2021**, *59*, 101970. [CrossRef] [PubMed]
2. Savini, G.; Giorgi, V.; Scarano, E.; Neri, D. Strawberry plant relationship through the stolon. *Physiol. Plant.* **2008**, *134*, 421–429. [CrossRef]
3. Díaz-García, G.; Enciso-Maldonado, G.A.; Díaz-García, L.A.; Legaria-Solano, J.P.; Bamberg, J.; Lozoya-Saldaña, H. Field Screening of *Solanum demissum* confirms its late blight resistance in the Toluca valley, Mexico. *Am. J. Potato Res.* **2024**, *101*, 122–131. [CrossRef]
4. Sanderson, M.A.; Byers, R.A.; Skinner, R.H.; Elwinger, G.F. Growth and complexity of white clover stolons in response to biotic and abiotic stress. *Crop Sci.* **2003**, *43*, 2197–2205. [CrossRef]
5. Pornaro, C.; Macolino, S.; Menegon, A.; Richardson, M. WinRHIZO technology for measuring morphological traits of bermudagrass stolons. *Agron. J.* **2017**, *109*, 3007–3010. [CrossRef]
6. Sishu, N.K.; Selvara, C.I.; Parasurama, D.S. A review of micropropagation of *Glycyrrhiza glabra* L. (Licorice). In *Micropropagation of Medicinal Plants*; Bentham Science Publishers: Sharjah, United Arab Emirates, 2024; pp. 267–282.
7. Gaston, A.; Perrotte, J.; Lerceteau-Köhler, E.; Rousseau-Gueutin, M.; Petit, A.; Hernould, M.; Rothan, C.; Denoyes, B. *PFRU*, a single dominant locus regulates the balance between sexual and asexual plant reproduction in cultivated strawberry. *J. Exp. Bot.* **2013**, *64*, 1837–1848. [CrossRef] [PubMed]
8. Park, Y.G.; Muneer, S.; Kim, S.; Hwang, S.J.; Jeong, B.R. Foliar or subirrigational silicon supply modulates salt stress in strawberry during vegetative propagation. *Hortic. Environ. Biotechnol.* **2018**, *59*, 11–18. [CrossRef]
9. Tsuruyama, J.; Shibuya, T. Growth and flowering responses of seed-propagated strawberry seedlings to different photoperiods in controlled environment chambers. *HortTechnology* **2018**, *28*, 453–458. [CrossRef]
10. Hammami, I.; Jellali, M.; Ksontini, M.; Rejeb, M. Propagation of the strawberry tree through seed (*Arbutus unedo*). *Int. J. Agric. Biol.* **2005**, *7*, 457–459.
11. Rho, I.R.; Woo, J.G.; Jeong, H.J.; Jeon, H.Y.; Lee, C.H. Characteristics of F1 hybrids and inbred lines in octoploid strawberry (*Fragaria* × *ananassa* Duchesne). *Plant Breed.* **2012**, *131*, 550–554. [CrossRef]
12. Zheng, J.; Ji, F.; He, D.; Niu, G. Effect of light intensity on rooting and growth of hydroponic strawberry runner plants in a LED plant factory. *Agronomy* **2019**, *9*, 875. [CrossRef]
13. Walter, M.; Snelling, C.; Boyd-Wilson, K.S.; Langford, G.I.; Williams, G. Evaluation of organic strawberry runner production. *HortTechnology* **2005**, *15*, 787–796. [CrossRef]
14. Momenpour, A.; Taghavi, T.S.; Manochehr, S. Effects of banzyladenine and gibberellin on runner production and some vegetative traits of three strawberry cultivars. *Afr. J. Agric. Res.* **2011**, *6*, 4357–4361.
15. Amin, B.; Qureshi, K.M.; Ghani, A.; Mahmood, A.; Shah, S.A.S.; Khan, M.F.; Khalid, S.; Iqbal, S.; Anwar, I. Effect of Different Environments and GA3 on Growth and Runners Production of Strawberry (*Frageria Ananasa*). *J. Pharm. Negat. Results* **2023**, *14*, 208–218.
16. Chawla, W.; Singh, S.K.; Bal, S. Evaluation of performance of strawberry cultivars for vegetative attributes and runner production. *Plant Arch.* **2020**, *20*, 3759–3762.
17. El-Deeb, A.; Mohamed, F. Runner production of strawberry plants in soilless suspended system: Nitrogen rate, GA_3 and genotype effects. *Hortscience J. Suez Canal Univ.* **2018**, *7*, 35–46. [CrossRef]
18. Avdiu, V.; Dragusha, B.; Hajra, E.; Hondolli, G. Effects of different substrates on the runner production of the June-bearing strawberry cv.'Senga Sengana'. *Hortic. Sci.* **2022**, *49*, 197–204. [CrossRef]
19. Savini, G.; Neri, D.; Zucconi, F.; Sugiyama, N. Strawberry growth and flowering: An architectural model. *Int. J. Fruit Sci.* **2005**, *5*, 29–50. [CrossRef]
20. Tenreira, T.; Lange, M.J.P.; Lange, T.; Bres, C.; Labadie, M.; Monfort, A.; Hernould, M.; Rothan, C.; Denoyes, B. A specific gibberellin 20-oxidase dictates the flowering-runnering decision in diploid strawberry. *Plant Cell* **2017**, *29*, 2168–2182. [CrossRef]
21. Feng, J.; Cheng, L.; Zhu, Z.; Yu, F.; Dai, C.; Liu, Z.; Guo, W.-W.; Wu, X.-M.; Kang, C. GRAS transcription factor *LOSS OF AXILLARY MERISTEMS* is essential for stamen and runner formation in wild strawberry. *Plant Physiol.* **2021**, *186*, 1970–1984. [CrossRef]
22. Andrés, J.; Andrés, F.; Hytönen, T.; Koskela, E. *Regulation of Axillary Bud Fate in Wild Strawberries*; Helsingin yliopisto: Helsinki, Finland, 2025.
23. Zhang, C.; Fan, L.; Le, B.H.; Ye, P.; Mo, B.; Chen, X. Regulation of *ARGONAUTE10* expression enables temporal and spatial precision in axillary meristem initiation in *Arabidopsis*. *Dev. Cell* **2020**, *55*, 603–616.e5. [CrossRef] [PubMed]
24. Aspuria, J.R.; Fujime, Y. Eco-physiological studies in the analysis of dormancy in strawberry. In Proceedings of the Dormancy and the Related Problems of Deciduous Fruit Trees 395, Kyoto, Japan, 21–27 August 1994; pp. 97–104.
25. Hytönen, T.; Elomaa, P. Genetic and environmental regulation of flowering and runnering in strawberry. *Genes Genomes Genom.* **2011**, *5*, 56–64.
26. Hytönen, T.; Kurokura, T. Control of flowering and runnering in strawberry. *Hortic. J.* **2020**, *89*, 96–107. [CrossRef]

27. Honjo, M.; Kataoka, S.; Yui, S.; Morishita, M.; Yano, T.; Hamano, M.; Yamazaki, H. Varietal differences and selection indicators for flowering pattern in everbearing strawberry. *J. Jpn. Soc. Hortic. Sci.* **2011**, *80*, 38–44. [CrossRef]
28. Yoshida, Y.; Nishimoto, T. Propagation and floral induction of transplant for forcing long-term production of seasonal flowering strawberries in Japan. *Hortic. J.* **2020**, *89*, 87–95. [CrossRef]
29. Heide, O.; Stavang, J.; Sønsteby, A. Physiology and genetics of flowering in cultivated and wild strawberries–a review. *J. Hortic. Sci. Biotechnol.* **2013**, *88*, 1–18. [CrossRef]
30. Hytönen, T.; Elomaa, P.; Moritz, T.; Junttila, O. Gibberellin mediates daylength-controlled differentiation of vegetative meristems in strawberry (*Fragaria*× *ananassa* Duch). *BMC Plant Biol.* **2009**, *9*, 18. [CrossRef]
31. Mouhu, K.; Kurokura, T.; Koskela, E.A.; Albert, V.A.; Elomaa, P.; Hytönen, T. The *Fragaria vesca* homolog of *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* represses flowering and promotes vegetative growth. *Plant Cell* **2013**, *25*, 3296–3310. [CrossRef] [PubMed]
32. Li, Y.; Xiao, J.; Hu, J.; Jeong, B.R. Critical photoperiod and optimal quality of night interruption light for runner induction in June-bearing strawberries. *Agronomy* **2021**, *11*, 1996. [CrossRef]
33. Hossain, M.R.; Natarajan, S.; Kim, H.-T.; Jesse, D.M.I.; Lee, C.-G.; Park, J.-I.; Nou, I.-S. High density linkage map construction and QTL mapping for runner production in allo-octoploid strawberry *Fragaria*× *ananassa* based on ddRAD-seq derived SNPs. *Sci. Rep.* **2019**, *9*, 3275. [CrossRef]
34. Rivero, R.; Remberg, S.F.; Heide, O.M.; Sønsteby, A. Environmental regulation of dormancy, flowering and runnering in two genetically distant everbearing strawberry cultivars. *Sci. Hortic.* **2021**, *290*, 110515. [CrossRef]
35. Sonsteby, A.; Nes, A. Short days and temperature effects on growth and flowering in strawberry (*Fragaria*× *ananassa* Duch.). *J. Hortic. Sci. Biotechnol.* **1998**, *73*, 730–736. [CrossRef]
36. Smeets, L. Runner formation on strawberry plants in autumn and winter: II. Influence of the light intensity on the photoperiodical behaviour. *Euphytica* **1955**, *4*, 240–244. [CrossRef]
37. Xu, X.; Hernandez, R. The effect of light intensity on vegetative propagation efficacy, growth, and morphology of "Albion" strawberry plants in a precision indoor propagation system. *Appl. Sci.* **2020**, *10*, 1044. [CrossRef]
38. Wu, C.; Hsu, S.; Chang, M.; Fang, W. Effect of light environment on runner plant propagation of strawberry. In Proceedings of the VI International Symposium on Light in Horticulture 907, Tsukuba, Japan, 15–19 November 2009; pp. 297–302.
39. Zheng, J.; He, D.; Ji, F. Effects of light intensity and photoperiod on runner plant propagation of hydroponic strawberry transplants under LED lighting. *Int. J. Agric. Biol. Eng.* **2019**, *12*, 26–31. [CrossRef]
40. Park, S.W.; Kwack, Y.; Chun, C. Growth of runner plants grown in a plant factory as affected by light intensity and container volume. *Hortic. Sci. Technol.* **2017**, *35*, 439–445. [CrossRef]
41. Aubé, M.; Roby, J.; Kocifaj, M. Evaluating potential spectral impacts of various artificial lights on melatonin suppression, photosynthesis, and star visibility. *PLoS ONE* **2013**, *8*, e67798. [CrossRef] [PubMed]
42. Dufault, R.J.; Ward, B.K. Further attempts to enhance forced 'Sweet Charlie' strawberry yield through manipulation of light quality in high tunnels. *Int. J. Fruit Sci.* **2009**, *9*, 409–418. [CrossRef]
43. Uddin, A.; Hoq, M.; Rini, S.; Urme, F.; Ahmad, H. Influence of supplement LED spectrum on growth and yield of Strawberry. *J. Biosci. Agr. Res* **2018**, *16*, 1348–1355. [CrossRef]
44. Yang, J.; Song, J.; Jeong, B.R. Flowering and runnering of seasonal strawberry under different photoperiods are affected by intensity of supplemental or night-interrupting blue light. *Plants* **2024**, *13*, 375. [CrossRef] [PubMed]
45. Heide, O.M.; Sønsteby, A. Interactions of temperature and photoperiod in the control of flowering of latitudinal and altitudinal populations of wild strawberry (*Fragaria vesca*). *Physiol. Plant.* **2007**, *130*, 280–289. [CrossRef]
46. Morrison, D.M.; Blankenship, E.E.; Read, P.E.; Paparozzi, E.T. Stolon development and cultural production practices of winter-grown strawberries. *Int. J. Fruit Sci.* **2018**, *18*, 138–152. [CrossRef]
47. Yanagi, T.; Oda, Y. Effects of chilling history on successive flowering and runner development of everbearing and non-everbearing strawberry cultivars. *J. Jpn. Soc. Hortic. Sci.* **1990**, *59*, 357–363. [CrossRef]
48. Watanabe, G.; Yanagi, T.; Okuda, N.; Saito, Y. Effect of cold storage duration on runner production in strawberry plants in winter. In Proceedings of the VI International Strawberry Symposium 842, Huelva, Spain, 3–7 March 2008; pp. 729–732.
49. Al-Madhagi, I.A.; Al-Munibary, M.; Al-Doubibi, M. Effect of chilling and accumulative photo-thermal units on flowering of strawberry (*Fragaria*× *Ananassa* Duch.). *J. Hortic. Res.* **2018**, *26*, 25–35. [CrossRef]
50. Sønsteby, A.; Heide, O.M. Dormancy relations and flowering of the strawberry cultivars Korona and Elsanta as influenced by photoperiod and temperature. *Sci. Hortic.* **2006**, *110*, 57–67. [CrossRef]
51. Hokanson, S.C.; Takeda, F.; Enns, J.M.; Black, B.L. Influence of plant storage duration on strawberry runner tip viability and field performance. *HortScience* **2004**, *39*, 1596–1600. [CrossRef]
52. Hamano, M.; Yamazaki, H.; Morishita, M.; Imada, S. Effect of chilling and day length on runner of everbearing type strawberry. In Proceedings of the VI International Strawberry Symposium 842, Huelva, Spain, 3–7 March 2008; pp. 671–674.

53. Lee, I.; Kim, H.-S.; Nam, M.H.; Oh, S.-K. Effect of cold storage method for 'Sulhyang' strawberry mother plants on mother plant growth and the number of runners and daughters. *Korean J. Agric. Sci.* **2020**, *47*, 625–632. [CrossRef]
54. Li, Y.; Hu, J.; Wei, H.; Jeong, B.R. A long-day photoperiod and 6-benzyladenine promote runner formation through upregulation of soluble sugar content in strawberry. *Int. J. Mol. Sci.* **2020**, *21*, 4917. [CrossRef] [PubMed]
55. Kurokura, T.; Iwama, T.; Inaba, Y.; Sugiyama, N. Effect of day-length on the developmental pattern of axillary buds in June-bearing strawberry plants. *J. Hortic. Sci. Biotechnol.* **2005**, *80*, 139–142. [CrossRef]
56. Sønsteby, A.; Heide, O. Flowering performance and yield of established and recent strawberry cultivars (*Fragaria× ananassa*) as affected by raising temperature and photoperiod. *J. Hortic. Sci. Biotechnol.* **2017**, *92*, 367–375. [CrossRef]
57. Chen, J.; Ji, F.; Gao, R.; He, D. Reducing red light proportion in full-spectrum LEDs enhances runner plant propagation by promoting the growth and development of mother plants in strawberry. *Front. Plant Sci.* **2024**, *15*, 1465004. [CrossRef]
58. Samad, S.; Rivero, R.; Kalyandurg, P.B.; Vetukuri, R.R.; Heide, O.M.; Sønsteby, A.; Khalil, S. Characterization of environmental effects on flowering and plant architecture in an everbearing strawberry F1-hybrid by meristem dissection and gene expression analysis. *Horticulturae* **2022**, *8*, 626. [CrossRef]
59. Durner, E.F. Photoperiod affects floral ontogeny in strawberry (*Fragaria× ananassa* Duch.) plug plants. *Sci. Hortic.* **2015**, *194*, 154–159. [CrossRef]
60. Sidhu, V.; Bernier-English, V.; Lamontagne-Drolet, M.; Gravel, V. Effect of light quality and extended photoperiod on flower bud induction during transplant production of day-neutral strawberry cultivars. *Can. J. Plant Sci.* **2021**, *102*, 356–367. [CrossRef]
61. Van Delm, T.; Melis, P.; Stoffels, K.; Baets, W. The effect of long-day treatment on runners and inflorescences on everbearing strawberry cultivar'Capri'. In Proceedings of the XXIX International Horticultural Congress on Horticulture: Sustaining Lives, Livelihoods and Landscapes (IHC2014): II 1117, Brisbane, Australia, 17 August 2014; pp. 285–290.
62. Bradford, E.; Hancock, J.F.; Warner, R.M. Interactions of temperature and photoperiod determine expression of repeat flowering in strawberry. *J. Am. Soc. Hortic. Sci.* **2010**, *135*, 102–107. [CrossRef]
63. Pipattanawong, N.; Fujishige, N.; Yamane, K.; Ijiro, Y.; Ogata, R. Effects of growth regulators and fertilizer on runner production, flowering, and growth in day-neutral strawberries [*Fragaria ananassa*]. *Jpn. J. Trop. Agric.* **1996**, *40*, 101–105.
64. Farjana, S.; Park, I.S.; Choi, J.M. Macro-Elements in liquid fertilization influence differently in occurrence and growth of runner plants in strawberry propagation. *Hortic. Sci. Technol.* **2025**, *43*, 21–32. [CrossRef]
65. Bakshi, P.; Jasrotia, A.; Sharma, A.; Rai, P.; Wali, V.; Kumar, R. Pre-harvest application of iron and zinc influences growth, yield, quality and runner production of strawberry (*Fragaria ananassa*) cv Chandler. *Indian J. Agric. Sci.* **2013**, *83*, 678–684.
66. Mohamed, R.; Abd El-Aal, H.; Abd El-Aziz, M. Effect of phosphorus, zinc and their interactions on vegetative growth characters, yield and fruit quality of strawberry. *J. Hortic. Sci. Ornam. Plants* **2011**, *3*, 106–114.
67. Poorter, H.; Niklas, K.J.; Reich, P.B.; Oleksyn, J.; Poot, P.; Mommer, L. Biomass allocation to leaves, stems and roots: Meta--analyses of interspecific variation and environmental control. *New Phytol.* **2012**, *193*, 30–50. [CrossRef]
68. Kurokura, T.; Samad, S.; Koskela, E.; Mouhu, K.; Hytönen, T. *Fragaria vesca CONSTANS* controls photoperiodic flowering and vegetative development. *J. Exp. Bot.* **2017**, *68*, 4839–4850. [CrossRef]
69. Gaston, A.; Potier, A.; Alonso, M.; Sabbadini, S.; Delmas, F.; Tenreira, T.; Cochetel, N.; Labadie, M.; Prévost, P.; Folta, K.M. The FveFT2 florigen/FveTFL1 antflorigen balance is critical for the control of seasonal flowering in strawberry while FveFT3 modulates axillary meristem fate and yield. *New Phytol.* **2021**, *232*, 372–387. [CrossRef]
70. Stewart, P.J.; Folta, K.M. A review of photoperiodic flowering research in strawberry (*Fragaria* spp.). *Crit. Rev. Plant Sci.* **2010**, *29*, 1–13. [CrossRef]
71. Rantanen, M.; Kurokura, T.; Jiang, P.; Mouhu, K.; Hytönen, T. Strawberry homologue of *TERMINAL FLOWER 1* integrates photoperiod and temperature signals to inhibit flowering. *Plant J.* **2015**, *82*, 163–173. [CrossRef]
72. Whitaker, V.M.; Knapp, S.J.; Hardigan, M.A.; Edger, P.P.; Slovin, J.P.; V Bassil, N.; Hytönen, T.; Mackenzie, K.K.; Lee, S.; Jung, S. A roadmap for research in octoploid strawberry. *Hortic. Res.* **2020**, *7*, 33. [CrossRef]
73. Pietikäinen, L. Flower Induction and Vegetative Growth Characteristics in *Fragaria× ananassa* Cultivars 'Calypso' and 'Hapil'. Master's Thesis, University of Helsinki, Helsinki, Finland, October 2021.
74. Kumar, R.; Bakshi, M.; Singh, D. Influence of plant growth regulators on growth, yield and quality of strawberrry (*Fragaria x ananassa* Duch.) under UP sub tropics. *Asian J. Hortic.* **2012**, *7*, 434–436.
75. Jamal Uddin, A.; Hossan, M.; Islam, M.; Ahsan, M.; Mehraj, H. Strawberry growth and yield responses to gibberellic acid concentrations. *J. Exp. Biosci.* **2012**, *3*, 51–56.
76. Palei, S.; Das, K.; Sahoo, K.; Dash, D.K.; Swain, S. Influence of plant growth regulators on strawberry Cv. Chandler under Odisha condition. *Int. J. Sci. Res* **2016**, *7*, 9945–9948.
77. Greene, D.W.; Schloemann, S.G. Prohexadione-calcium inhibits runner formation and enhances yield of strawberry. *J. Am. Pomol. Soc.* **2010**, *64*, 125–139.
78. Kim, H.M.; Lee, H.R.; Kang, J.H.; Hwang, S.J. Prohexadione-calcium application during vegetative growth affects growth of mother plants, runners, and runner plants of Maehyang strawberry. *Agronomy* **2019**, *9*, 155. [CrossRef]

79. Surapornpiboon, P.; Surapornpiboon, P. Effect of benzyladenine and gibberellic acid on runner production in strawberry. In Proceedings of the 19th Rajamangala University of Technology Conference, Pathum Thani, Thailand, 22–27 January 2002.
80. Bagheri, M.; Mansouri, H. Effect of induced polyploidy on some biochemical parameters in *Cannabis sativa* L. *Appl. Biochem. Biotechnol.* **2015**, *175*, 2366–2375. [CrossRef]
81. Dai, F.; Wang, Z.; Luo, G.; Tang, C. Phenotypic and transcriptomic analyses of autotetraploid and diploid mulberry (*Morus alba* L.). *Int. J. Mol. Sci.* **2015**, *16*, 22938–22956. [CrossRef]
82. Qiu, Y.; Guan, S.C.; Wen, C.; Li, P.; Gao, Z.; Chen, X. Auxin and cytokinin coordinate the dormancy and outgrowth of axillary bud in strawberry runner. *BMC Plant Biol.* **2019**, *19*, 528. [CrossRef]
83. Booker, J.; Chatfield, S.; Leyser, O. Auxin acts in xylem-associated or medullary cells to mediate apical dominance. *Plant Cell* **2003**, *15*, 495–507. [CrossRef]
84. Kour, S.; Kumar, R.; Wali, V.; Sharma, A.; Bakshi, P. Impact of benzyladenine and gibberellic acid on quality and economics of runner production in Chandler strawberry (*Fragaria× ananassa*) under subtropical climate. *Indian J. Agric. Sci* **2017**, *87*, 964–967. [CrossRef]
85. Kahangi, E.; Fujime, Y.; Nakamura, E. Effects of chilling and growth regulators on runner production of three strawberry cultivars under tropical conditions. *J. Hortic. Sci.* **1992**, *67*, 381–384. [CrossRef]
86. Liu, C.; Guo, Z.; Park, Y.G.; Wei, H.; Jeong, B.R. PGR and its application method affect number and length of runners produced in 'Maehyang' and 'Sulhyang' strawberries. *Agronomy* **2019**, *9*, 59. [CrossRef]
87. Li, Y.; Hu, J.; Xiao, J.; Guo, G.; Jeong, B.R. Foliar thidiazuron promotes the growth of axillary buds in Strawberry. *Agronomy* **2021**, *11*, 594. [CrossRef]
88. Gomez-Roldan, V.; Fermas, S.; Brewer, P.B.; Puech-Pagès, V.; Dun, E.A.; Pillot, J.-P.; Letisse, F.; Matusova, R.; Danoun, S.; Portais, J.-C. Strigolactone inhibition of shoot branching. *Nature* **2008**, *455*, 189–194. [CrossRef]
89. Leyser, H.; de Saint Germain, A.; Waldie, T.; Troadec, C.; Citerne, S.; Kadakia, N.; Pillot, J.-P.; Prigge, M.; Aubert, G.; Bendahmane, A. The pea branching *RMS2* gene encodes the *PsAFB4/5* auxin receptor and is involved in an auxin-strigolactone regulation loop. *PLoS Genet.* **2018**, *13*, e1007089.
90. Zhu, Y.; Wagner, D. Plant inflorescence architecture: The formation, activity, and fate of axillary meristems. *Cold Spring Harb. Perspect. Biol.* **2020**, *12*, a034652. [CrossRef] [PubMed]
91. Peng, Y.; Jiang, Y.; He, C.; She, M.; Li, M.; Chen, Q.; Zhang, Y.; Lin, Y.; Zhang, Y.; Wang, Y. Exogenous GR24 inhibits strawberry tillering by affecting the phytohormone signaling and sugar metabolism pathways. *Agronomy* **2023**, *13*, 3078. [CrossRef]
92. Kender, W.; Carpenter, S.; Braun, J. Runner formation in everbearing strawberry as influenced by growth-promoting and inhibiting substances. *Ann. Bot.* **1971**, *35*, 1045–1052. [CrossRef]
93. Yao, C.; Finlayson, S.A. Abscisic acid is a general negative regulator of Arabidopsis axillary bud growth. *Plant Physiol.* **2015**, *169*, 611–626. [CrossRef]
94. Wang, L.; Wang, B.; Yu, H.; Guo, H.; Lin, T.; Kou, L.; Wang, A.; Shao, N.; Ma, H.; Xiong, G. Transcriptional regulation of strigolactone signalling in *Arabidopsis*. *Nature* **2020**, *583*, 277–281. [CrossRef]
95. Luo, Z.; Janssen, B.J.; Snowden, K.C. The molecular and genetic regulation of shoot branching. *Plant Physiol.* **2021**, *187*, 1033–1044. [CrossRef]
96. Aguilar-Martínez, J.A.; Poza-Carrion, C.; Cubas, P. *Arabidopsis BRANCHED1* acts as an integrator of branching signals within axillary buds. *Plant Cell* **2007**, *19*, 458–472. [CrossRef] [PubMed]
97. Li, W.; Wang, B.; Sun, H.; Zhang, Z. Transcriptome profiling of runner formation induced by exogenous gibberellin in *Fragaria vesca*. *Sci. Hortic.* **2021**, *281*, 109966. [CrossRef]
98. Kim, Y.J.; Kim, H.M.; Kim, H.M.; Hwang, S.J. Growth and runner production of 'Maehyang' strawberry as affected by application method and concentration of cytokinin. *J. Bio-Environ. Control* **2017**, *26*, 72–77. [CrossRef]
99. Deyton, D.E.; Sams, C.E.; Cummins, J.C. Strawberry growth and photosynthetic responses to paclobutrazol. *HortScience* **1991**, *26*, 1178–1180. [CrossRef]
100. Lan, G.; Wu, M.; Zhang, Q.; Yuan, B.; Shi, G.; Zhu, N.; Zheng, Y.; Cao, Q.; Qiao, Q.; Zhang, T. Transcriptomic and physiological analyses for the role of hormones and sugar in axillary bud development of wild strawberry stolon. *Plants* **2024**, *13*, 2241. [CrossRef]
101. Wang, M.; Pérez-Garcia, M.-D.; Davière, J.-M.; Barbier, F.; Ogé, L.; Gentilhomme, J.; Voisine, L.; Péron, T.; Launay-Avon, A.; Clément, G. Outgrowth of the axillary bud in rose is controlled by sugar metabolism and signalling. *J. Exp. Bot.* **2021**, *72*, 3044–3060. [CrossRef]
102. Kebrom, T.H.; Doust, A.N. Activation of apoplastic sugar at the transition stage may be essential for axillary bud outgrowth in the grasses. *Front. Plant Sci.* **2022**, *13*, 1023581. [CrossRef]
103. Liu, W.; Peng, B.; Song, A.; Jiang, J.; Chen, F. Sugar transporter, CmSWEET17, promotes bud outgrowth in *Chrysanthemum morifolium*. *Genes* **2020**, *11*, 26. [CrossRef] [PubMed]

104. Bertheloot, J.; Schneider, A.; Ledroit, L.; Perez-Garcia, M.-D.; Boudon, F.; Godin, C.; Sakr, S. Axillary bud outgrowth regulation by light intensity: Modelling hormone and sugar interactions. In Proceedings of the International Conference on Functional-Structural Plant Models (FSPM 2020), Germany, Hannover, 5–9 October 2020.
105. Bertheloot, J.; Barbier, F.; Boudon, F.; Perez-Garcia, M.D.; Péron, T.; Citerne, S.; Dun, E.; Beveridge, C.; Godin, C.; Sakr, S. Sugar availability suppresses the auxin--induced strigolactone pathway to promote bud outgrowth. *New Phytol.* **2020**, *225*, 866–879. [CrossRef] [PubMed]
106. Salam, B.B.; Barbier, F.; Danieli, R.; Teper-Bamnolker, P.; Ziv, C.; Spíchal, L.; Aruchamy, K.; Shnaider, Y.; Leibman, D.; Shaya, F. Sucrose promotes stem branching through cytokinin. *Plant Physiol.* **2021**, *185*, 1708–1721. [CrossRef]
107. Bird, K.A.; Hardigan, M.A.; Ragsdale, A.P.; Knapp, S.J.; VanBuren, R.; Edger, P.P. Diversification, spread, and admixture of octoploid strawberry in the Western Hemisphere. *Am. J. Bot.* **2021**, *108*, 2269–2281. [CrossRef]
108. Edger, P.P.; Poorten, T.J.; VanBuren, R.; Hardigan, M.A.; Colle, M.; McKain, M.R.; Smith, R.D.; Teresi, S.J.; Nelson, A.D.; Wai, C.M. Origin and evolution of the octoploid strawberry genome. *Nat. Genet.* **2019**, *51*, 541–547. [CrossRef]
109. Koskela, E.A.; Hytönen, T. Control of flowering in strawberries. In *The Genomes of Rosaceous Berries and Their Wild Relatives*; Springer: Cham, Switzerland, 2018; pp. 35–48.
110. Caruana, J.C.; Sittmann, J.W.; Wang, W.; Liu, Z. Suppressor of runnerless encodes a DELLA protein that controls runner formation for asexual reproduction in strawberry. *Mol. Plant* **2018**, *11*, 230–233. [CrossRef]
111. Joldersma, D.; Sadowski, N.; Timp, W.; Liu, Z. Assembly and annotation of *Fragaria vesca* 'Yellow Wonder' genome, a model diploid strawberry for molecular genetic research. *Fruit Res.* **2022**, *2*, 13. [CrossRef]
112. Newton, A.; Duncan, J.; Augustin, N.H.; Guy, D.; Cooke, D. Survival, distribution and genetic variability of inoculum of the strawberry red core pathogen, *Phytophthora fragariae* var. fragariae, in soil. *Plant Pathol.* **2010**, *59*, 472–479. [CrossRef]
113. Alger, E.I.; Platts, A.E.; Deb, S.K.; Luo, X.; Ou, S.; Cao, Y.; Hummer, K.E.; Xiong, Z.; Knapp, S.J.; Liu, Z. Chromosome-scale genome for a red-fruited, perpetual flowering and runnerless woodland strawberry (*Fragaria vesca*). *Front. Genet.* **2021**, *12*, 671371. [CrossRef] [PubMed]
114. Hjalmarsson, I. Strawberry cultivars preserved in the Swedish National Gene Bank. In Proceedings of the Latvian Academy of Sciences, Lomma, Sweden, 15 July 2022; pp. 402–408.
115. Martins, A.O.; Nunes-Nesi, A.; Araújo, W.L.; Fernie, A.R. To bring flowers or do a runner: Gibberellins make the decision. *Mol. Plant* **2018**, *11*, 4–6. [CrossRef]
116. Li, W.; Zhang, J.; Sun, H.; Wang, S.; Chen, K.; Liu, Y.; Li, H.; Ma, Y.; Zhang, Z. FveRGA1, encoding a DELLA protein, negatively regulates runner production in *Fragaria vesca*. *Planta* **2018**, *247*, 941–951. [CrossRef] [PubMed]
117. Zhang, Q.Q.; Wang, J.G.; Wang, L.Y.; Wang, J.F.; Wang, Q.; Yu, P.; Bai, M.Y.; Fan, M. Gibberellin repression of axillary bud formation in *Arabidopsis* by modulation of DELLA-SPL9 complex activity. *J. Integr. Plant Biol.* **2020**, *62*, 421–432. [CrossRef]
118. Li, Y.; Xia, T.; Gao, F.; Li, Y. Control of plant branching by the CUC2/CUC3-DA1-UBP15 regulatory module. *Plant Cell* **2020**, *32*, 1919–1932. [CrossRef]
119. Zheng, C.; Kwame Acheampong, A.; Shi, Z.; Halaly, T.; Kamiya, Y.; Ophir, R.; Galbraith, D.W.; Or, E. Distinct gibberellin functions during and after grapevine bud dormancy release. *J. Exp. Bot.* **2018**, *69*, 1635–1648. [CrossRef]
120. Raman, S.; Greb, T.; Peaucelle, A.; Blein, T.; Laufs, P.; Theres, K. Interplay of miR164, *CUP-SHAPED COTYLEDON* genes and *LATERAL SUPPRESSOR* controls axillary meristem formation in *Arabidopsis thaliana*. *Plant J.* **2008**, *55*, 65–76. [CrossRef]
121. Zheng, G.; Wei, W.; Li, Y.; Kan, L.; Wang, F.; Zhang, X.; Li, F.; Liu, Z.; Kang, C. Conserved and novel roles of miR164--CUC 2 regulatory module in specifying leaf and floral organ morphology in strawberry. *New Phytol.* **2019**, *224*, 480–492. [CrossRef]
122. Cao, X.; Jiao, Y. Control of cell fate during axillary meristem initiation. *Cell. Mol. Life Sci.* **2020**, *77*, 2343–2354. [CrossRef] [PubMed]
123. Sooriyapathirana, S.S.; Mookerjee, S.; Weebadde, C.K.; Finn, C.E.; Lewers, K.; Bushakra, J.M.; Luby, J.J.; Stewart, P.; Neils, S.; Hancock, J.F. Identification of QTL associated with flower and runner production in octoploid strawberry (*Fragaria* × *ananassa*). *J. Berry Res.* **2015**, *5*, 107–116. [CrossRef]
124. Cockerton, H.M.; Nellist, C.F.; Hytönen, T.; Litthauer, S.; Hopson, K.; Whitehouse, A.; Sobczyk, M.; Harrison, R.J. Epistatic modifiers influence the expression of continual flowering in strawberry. *Plants People Planet* **2023**, *5*, 70–81. [CrossRef]
125. Samad, S.; Kurokura, T.; Koskela, E.; Toivainen, T.; Patel, V.; Mouhu, K.; Sargent, D.J.; Hytönen, T. Additive QTLs on three chromosomes control flowering time in woodland strawberry (*Fragaria vesca* L.). *Hortic. Res.* **2017**, *4*, 17020. [CrossRef]
126. Saiga, S.; Tada, M.; Segawa, T.; Nishikawa, M.; Makita, N.; Sakamoto, M.; Tanaka, K.; Wada, T.; Takagi, H. NGS-based genome wide association study helps to develop co-dominant marker for the physical map-based locus of PFRU controlling flowering in cultivated octoploid strawberry. *Euphytica* **2023**, *219*, 6. [CrossRef]
127. Liang, J.; Wu, Z.; Zheng, J.; Koskela, E.A.; Fan, L.; Fan, G.; Gao, D.; Dong, Z.; Hou, S.; Feng, Z. The GATA factor *HANABA TARANU* promotes runner formation by regulating axillary bud initiation and outgrowth in cultivated strawberry. *Plant J.* **2022**, *110*, 1237–1254. [CrossRef]

128. Park, S.W. Establishment of a Propagation System for Strawberry Using a Plant Factory with Artificial Lighting. Doctoral Thesis, Seoul National University, Seoul, Republic of Korea, February 2018.
129. Lee, H.; Park, S.W.; Cui, M.; Lee, B.; Minh Pham, D.; Hwang, H.; Chun, C. Improvement of strawberry transplant production efficiency by supplementary blue light in a plant factory using white LEDs. *Hortic. Environ. Biotechnol.* **2023**, *64*, 233–244. [CrossRef]
130. Roszak, P.; Heo, J.O.; Blob, B.; Toyokura, K.; Sugiyama, Y.; de Luis Balaguer, M.A.; Lau, W.W.Y.; Hamey, F.; Cirrone, J.; Madej, E.; et al. Cell-by-cell dissection of phloem development links a maturation gradient to cell specialization. *Science* **2021**, *374*, eaba5531. [CrossRef] [PubMed]