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Developmental regulation of stolon and rhizome

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Stolons and rhizomes are modified stems for vegetative reproduction. While stolons grow above the ground, rhizomes grow beneath the ground. Stolons and rhizomes maintain the genotypes of hybrids and hence are invaluable for agricultural propagation. Diploid strawberry is a model for studying stolon development. At the axillary meristems, gibberellins and MADS box gene *SOC1* promote stolon formation, while the DELLA repressor inhibits stolon development. Photoperiod regulates stolon formation through regulating GA biosynthesis or balancing asexual with sexual mode of reproduction in the axillary meristems. In rhizomatous wild rice, the *BLADE-ON-PETIOLE* gene promotes sheath-to-blade ratio to confer rhizome tip stiffness and support underground growth. Together, this review aims to encourage further investigations into stolon and rhizome to benefit agriculture and environment.

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Introduction

Stolons and rhizomes are means of asexual reproduction, enabling plants to produce large numbers of clones effectively. Plants endowed with this ability are referred to as stoloniferous (stolon-forming) or rhizomatous (rhizome-forming) and they span across wide ecological habitats and plant taxa (Table 1; Table S1 for a more extensive list). Some species can even develop both stolons and rhizomes. However, the established model systems Arabidopsis, tomato, and rice do not develop stolon/rhizome; the molecular mechanisms underlying stolon/rhizome development are, therefore, poorly understood. This review mainly focuses on recent progress in understanding hormonal and environmental regulation of stolon development in diploid strawberry as well as molecular investigations of rhizome development in several rhizomatous species.

A stolon is a stem that grows horizontally above ground, producing a daughter plant (ramets or clonal plants) at the end (Figure 1a). Stolons are also referred to as runners, as if the daughter plants run away from the mother plant. Developmentally speaking, each sympodial stolon consists of two elongated internodes with a daughter plant at the second node (Figure 1a). The first node normally stays dormant while the axillary bud in the second node produces the next sympodial stolon. Therefore, while the stolon appears continuous with repeating units, it is actually derived from a linear series of sympodial stolons. Strawberry (*Fragaria* × *ananassa*) and bermudagrass (*Cynodon dactylon*) are some of the more familiar stoloniferous species (Table 1).

Like stolons, rhizomes are modified stems growing horizontally except that rhizomes grow under the ground (Figure 1b). Rhizomes also initiate from axillary buds of the mother plant. The apical meristem of rhizomes is covered by several layers of scale leaves that protect the meristem and help push through the soil. The rhizome meristem either produces a node or enters a developmental transition in which the rhizome tip bends upwards to produce an aerial shoot, a vegetative clone of the mother plant [1••]. The nodes in both stolon and rhizome produce adventitious roots to extend plants' root system. Examples of the rhizome-forming species are ginger (*Zingiber officinale*), wild sorghum (*Sorghum propinquum*), and lotus (*Nelumbo nucifera*) (Table 1).

Stolons and rhizomes are of significant agricultural and ecological importance

In some crop species, stolons and rhizomes enlarge to form a nutrient storage organ that is harvested for food. In potato (*Solanum tuberosum*), the tips of underground stolons enlarge and produce starchy tubers, a process referred to as tuberization, which contributes to potato as the third most important food crop in the world [2]. Therefore, extensive molecular genetic studies of tuberization, a process downstream of stolon initiation, have led to the discovery of long distance signaling between leaf and stolon tip in tuber formation [2,3]. Similarly, the rhizomes of lotus (*N. nucifera*) are rich in starch and other nutrients and are popular as a vegetable in China [4]. Ginger (*Z. officinale*) and turmeric (*Curcuma longa*) accumulate secondary metabolites such as curcuminoids, gingerols, and terpenoids in their rhizomes and are used as spices and in traditional Eastern medicine [5].

Stolons and rhizomes offer a tremendous advantage in vegetative propagation. Planting of rhizome fragments is the main mode of agricultural propagation for lotus,

Table 1

Representative stoloniferous and rhizomatous species.

Scientific name	Common name	Family	Stolon/ rhizome	Reference	Notes
Alternanthera philoxeroides	Alligatorweed	Amaranthaceae	Stolons	[15]	Invasive on several continents
Asparagus officinalis	Garden asparagus	Asparagaceae	Rhizomes	[51]	Perennial vegetable
Cardamine amara	Large bitter-cress	Brassicaceae	Rhizomes	[52]	Widespread across most of central Europe, extending into parts of Asia
Curcuma longa	Turmeric	Zingiberaceae	Rhizomes	[5]	Edible rhizome used as spice, traditional medicine
Cynodon dactylon	Bermudagrass	Poaceae	Stolons and rhizomes	[53]	Turfgrass, considered noxious in several states in the US
Fragaria × ananassa	Garden strawberry	Rosaceae	Stolons	[18]	Cultivated strawberry
Fragaria pentaphylla	Five-leaf strawberry	Rosaceae	Stolons	[32•]	Diploid species of wild strawberry native to China, leaf has five leaflets
Fragaria vesca	Woodland strawberry	Rosaceae	Stolons	[18]	Edible fruits, a model system for research
Houttuynia cordata	Chameleon plant	Saururaceae	Rhizomes	[42••]	Invasive in US, medicinal plant
Hydrocotyle vulgaris	European marsh pennywort	Araliaceae	Stolons	[14]	Invasive in China
Leymus triticoides	Creeping wildrye	Poaceae	Rhizomes	[54]	Native to North America, primarily used for soil stabilization
Mentha × piperita	Peppermint	Lamiaceae	Rhizomes	[55]	Aromatic plant, has culinary use
Musa accuminata	Banana	Musaceae	Rhizomes	[56]	Parent of cultivated banana
Nelumbo nucifera	Lotus	Nelumbonaceae	Rhizomes	[57]	Aquatic plant, edible rhizomes and seeds
Oryza longistaminata	Longstamen rice	Poaceae	Rhizomes	[7]	Wild relative of cultivated rice, perennial
Phyllostachys edulis	Moso bamboo	Bambusoideae	Rhizomes	[58]	Edible shoots, mostly commonly used in bamboo textile industry of China
Poa pratensis	Kentucky bluegrass	Poaceae	Rhizomes	[41]	Turfgrass
Rheum rhabarbarum	Rhubarb	Polygonaceae	Rhizomes	[59]	Perennial vegetable for which rhizome division is the main mode of propagation
Solanum tuberosum	Cultivated potato	Solanaceae	Stolons	[2,3]	Tubers are a food staple
Sorghum propinquum	Wild Sorghum	Poaceae	Rhizomes	[7]	A wild relative of sorghum, perennial
Trifolium repens	White clover	Fabaceae	Stolons	[60]	Important pasture legume
Zea diploperennis	Perennial teosinte	Poaceae	Rhizomes	[61]	Diploid, maize relative, rhizomes enable perenniality
Zingiber officinale	Ginger	Zingiberaceae	Rhizomes	[5]	Edible rhizome
Zoysia matrella	Manila grass	Poaceae	Stolons	[42••]	Turfgrass

ginger, turmeric, and potato. In cultivated strawberry (*Fragaria × ananassa*), an allo-octoploid with combination of four ancestral genomes [6], propagation through runners is essential to maintain the superior hybrid genotype that would otherwise be lost if the plants are propagated via seeds.

Rhizomatousness is closely connected to a perennial life strategy. Rhizomes store and allocate nutrients for perennial growth and protect dormant buds underground for overwintering. Interestingly, rhizomatous trait is absent in grain-producing annual plants such as sorghum, rice, and maize, yet each of them has a closely related, perennial, and rhizomatous relative, *S. propinquum*, *Oryza longistaminata*, and *Zea diploperennis*, respectively (Table 1). The close correlation between most rhizome-forming quantitative trait loci (QTLs) in sorghum and rice suggests that some of the same genes may influence rhizomatous trait in these distantly related grass species, lending the support that cultivated sorghum and rice, which have an annual habit, may have arisen from their perennial, rhizomatous ancestors through mutations in similar genes [7,8••].

In addition to their agricultural importance, stolons and rhizomes provide ecological advantages. The rhizome or stolon connecting two clones allows them to share resources, a process known as clonal integration, which enables plants to survive in heterogeneous environments and support young ramets before root establishment. Furthermore, initiating stolon development increases a plant's chance of reaching sunlight [9]. In some bermudagrass genotypes (*Cynodon* spp.), the large rhizome network contributes to their high drought tolerance [10]. Clonal plants in inland dunes were shown to better cope with animal grazing than non-clonal plants [11]. The

Figure 1

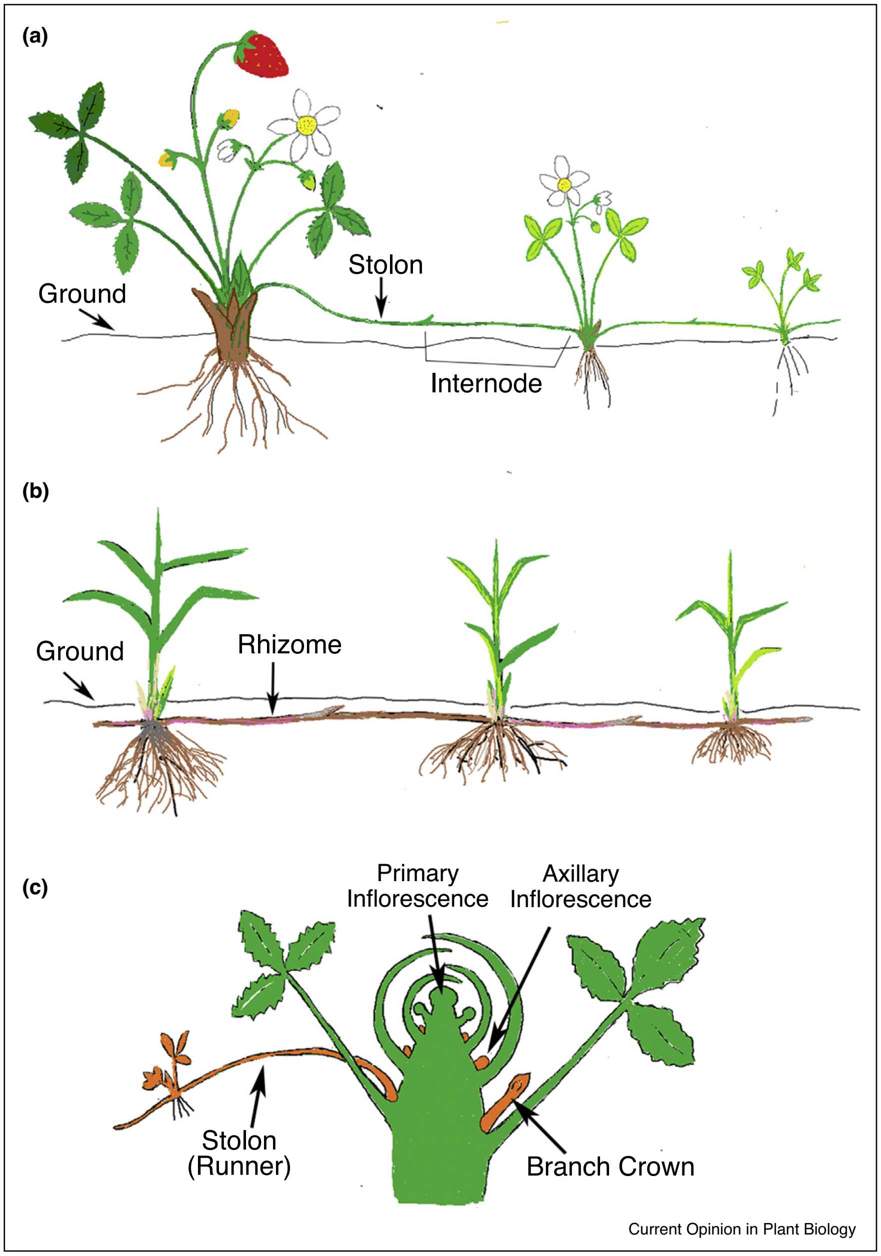

Illustration of stolon and rhizome.
(a) A diagram of a strawberry plant that develops a stolon above the ground. A dormant node between two daughter plants.
(b) A diagram of a grass that develops a rhizome that runs parallel beneath the ground. A dormant node between two daughter plants.
(c) A diagram of the primary crown of a strawberry. Axillary meristems (AXM) in the axils of leaves are marked in orange color. Stolon/runner, branch crown, and axillary inflorescence are alternative developmental fates for an AXM. The fourth option for AXM is to remain dormant.

clonal growth habit provides a means of prolonged survival and vegetative spread [12].

Importantly, many invasive species that threaten global biodiversity and agriculture also reproduce clonally through stolons and rhizomes (Table S1). Clonal integration is particularly beneficial to invasive plants in heterogeneous environments because carbohydrates, nutrients, and other resources can pass from a ramet in resource-rich conditions to a ramet in resource-poor conditions [13]. Compared to their close noninvasive relatives, invasive plants in China such as stoloniferous *Hydrocotyle vulgaris* are found to obtain greater benefits from clonal integration, a factor that may contribute to their success in heterogeneous environments [14]. Even in homogeneous conditions, sharing of resources in the invasive wetland plant *Alternanthera philoxeroides* can increase young ramet biomass through developmentally programmed division of labor, in which older ramets with more established root systems specialize in acquiring water and soil nutrients and younger ramets specialize in photosynthesis [15]. Since clonal propagation is a good predictor of species invasiveness [11,16], an understanding of rhizome and stolon development will enable better control of clonally propagating invasive plants.

Diploid strawberry as a model for studying stolon development

Strawberry, a member of the Rosaceae family, is an important fruit crop and a perennial rosette herb [17]. Because of the allo-octoploidy, the cultivated strawberry (*Fragaria* × *ananassa*) is a difficult system for genetic studies. Therefore, most of our current understanding of genetic control of stolon development is achieved in *Fragaria vesca*, a diploid strawberry.

In strawberry, the rosette stem (called crown) of the mother plant consists of short internodes (Figure 1c). The apical meristem of the rosette develops into a determinate inflorescence. The axillary meristem (AXM) at the axil of each rosette leaf has four alternative developmental fates. It can develop into a stolon for asexual reproduction, axillary inflorescence shoots for sexual reproduction, a branch crown which is a vegetative rosette, or remain in a dormant state (Figure 1c) [18]. While the stolon is a horizonal stem, the axillary inflorescence shoots and the branch crown (bearing a similar architecture as the mother plant), are upright. Since they all develop from AXMs, the trade-off between stolon-based vegetative reproduction and branch crown/inflorescence shoot-based fruit production is highly relevant to agricultural practices. The fruit yield is dependent on the development of inflorescence shoots and branch crowns while the plant propagation relies on runners. The phytohormone gibberellic acid (GA) and environmental signals including photoperiod and temperature influence which developmental fate an AXM takes.

Much like the axillary buds of strawberry with alternative fates, in rhizomatous grasses, an axillary bud can differentiate into a rhizome or a tiller. While rhizomes store and allocate nutrients for perennial growth, tillers produce inflorescences and seeds and are subject to senescence. Interestingly, in both stoloniferous and rhizomatous plants, differentiation of axillary buds is position-dependent, with basal axillary buds producing stolons or rhizomes and upper buds producing branch crowns, axillary inflorescences, or tillers [19,20,21••]. This suggests the involvement of developmental signals in AXM fate determination.

Phytohormone GA promotes stolon formation in strawberry

GA is an important phytohormone that controls multiple aspects of plant growth and development. GA biosynthesis enzyme gibberellin 20-oxidase (GA20ox) converts GA53 or GA12 respectively to GA20 or GA9, and gibberellin 3-oxidase (GA3ox) converts GA20 or GA9 to bioactive GA1 or GA4 [22]. In strawberry, exogenous application of GA can induce stolon formation. In contrast, application of prohexadione-calcium (Pro-Ca), an inhibitor of GA-3-oxidase, inhibits stolon formation and the inhibitory effect can be reversed by the application of GA [23,24]. However, the rescue effect of GA is not effective under SD condition, suggesting that in addition to the GA level in AXM, photoperiod may affect the sensitivity of the AXM to GA [24].

In *F. vesca*, several naturally occurring 'Alpine' strawberries, such as Yellow Wonder, Rügen, and Reine de Vallees, exhibit a runnerless (lack of runner) phenotype, and the single *runnerless* locus was mapped to Chr. 2 [25]. Exogenous application of GA was able to rescue the phenotype [21••,23,26]. Genetic mapping showed a tight linkage between the runnerless phenotype and an in-frame 9-bp deletion in *FveGA20ox4*, a variant that is present in all *runnerless* Alpine strawberries. *FveGA20ox4* is specifically expressed in the axillary meristems [21••], supporting that *FveGA20ox4* is probably the *RUNNERLESS* gene and that AXM-specific GA biosynthesis is essential for stolon formation.

After biosynthesis, GA is known to bind its receptor GID1. The binding facilitates the interaction between GID1 and the N-terminal DELLA domain of a repressor protein. This GA-mediated interaction between GID1 and DELLA leads to protein–protein interaction between DELLA and the F-box protein SLY1/GID2 and subsequent degradation of DELLA via ubiquitination [27,28]. The degradation of DELLA lifts repression of GA responses. In *F. vesca*, among five putative DELLA proteins, FveRGA1 is the only one that contains the full DELLA motif at its N terminus [29••]. Through a chemical mutagenesis screen of the *runnerless* Alpine strawberry Yellow Wonder, a mutant was identified that regained the ability to develop runners (Figure 2) [29••]. This mutation, named as *suppressor of runnerless* (*srl-1*), is a nonsense mutation at the C-terminal SAW domain of FveRGA1. In addition to the ability to develop constitutive runners in the *runnerless* background, the *srl-1* mutation caused elongated internodes in the main crown and severely reduced number of branch crowns. These phenotypes are consistent with constitutive GA responses in the absence of the DELLA repressor. The important role of *FveRGA1* in repressing runner formation is supported by RNAi silencing of *FveRGA1*, which restored stolon development in *runnerless* background [30•]. Hence, *FveRGA1* may encode a molecular switch between stolon and branch crown.

Figure 2

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A *runnerless* Alpine strawberry and a *suppressor of runnerless* (*srl-1*) mutant in the *runnerless* background.
Note the bushiness of the *runnerless* plant due to the development of multiple flowering branch crowns.

Interestingly, the *srl-1* mutant resembles the *arborea* mutant described previously [31] which was found in the island of Madeira. The mutant has longer internodes in main crown, produced only runners and no branch crowns, and the runner initiation was constitutive, independently of daylength. This *arborea* mutation was epistatic to the *runnerless* genotype when double mutants were constructed [31], much like the epistatic relation of *srl-1* to *runnerless* [29••]. Therefore, *arborea* is likely a naturally occurring mutation in the *FveRGA1* gene and should be tested if the germplasm can be recovered.

Another wild strawberry, *Fragaria pentaphylla*, produces a monopodial type of stolon, where a non-dormant bud develops at every node of the stolon after the first dormant node [32•]. Comparisons of transcriptomes between the dormant and non-dormant buds at the nodes of stolons in *F. vesca* and *F. pentaphylla*, combined with application of auxin, cytokinin, and auxin transport inhibitors, showed that auxin is involved in maintaining axillary bud dormancy while cytokinin promotes the axillary bud outgrowth [32•].

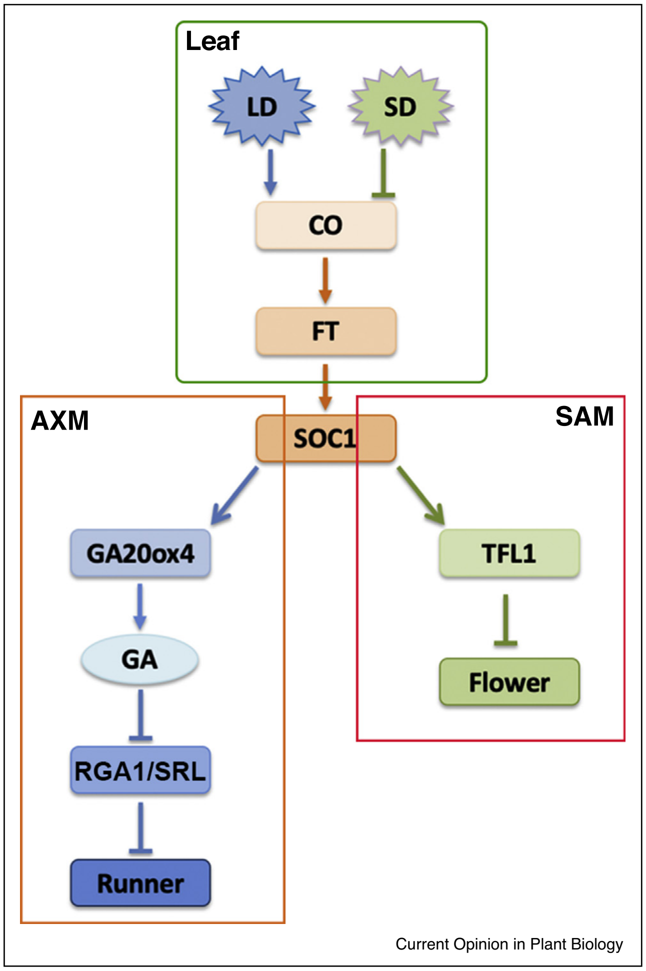
Photoperiod regulation of stolon development

In strawberry, stolon development is intimately connected with flowering. In most cases, they are oppositely influenced by the same environmental signal. Currently, most of our understanding relates to photoperiod, even though temperature plays an equally important role. In wild-type *F. vesca* (seasonal flowering strawberry) accessions, short-day (SD) and low temperature induce flowering and inhibit stolons [24,33••]. In contrast, long-day (LD) and high temperature inhibit flowering and induce stolons.

In *F. vesca f. semperflorens* (perpetual-flowering) accessions, flowering is continuous [25,34]. This perpetual flowering phenotype was caused by a recessive mutation in the *SEASONAL FLOWERING LOCUS* (*SFL*) [34]. Genetic mapping identified a 2-bp deletion in the first exon of *FveTFL1*, which is tightly linked with the perpetual flowering trait [35,36]. *35S*::*FveTFL1* prevented flowering in perpetual flowering accession Hawaii4, while silencing of *FveTFL1* in the seasonal flowering accession led to daylength-independent flowering, demonstrating that *FveTFL1* is the *SFL* [36]. While *FveTFL1* encodes a repressor of flowering in strawberry, it does not affect stolon development [36] (Figure 3).

MADS-box gene *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) appears to mediate the effect of photoperiod on both flowering and stolon formation in wild-type *F. vesca*. Under LD condition, *FveSOC1* is activated in shoot apical meristem (SAM) to activate the expression of *FveTFL1* which represses flowering. LD-activated *FveSOC1* activates the expression of GA biosynthesis genes including *FveGA20ox4* in AXM to induce stolon formation [33••]. Hence, *FveSOC1* is the key conduit between photoperiod and downstream developmental pathways (Figure 3). The coordinated regulation of flowering and runnering by *FveSOC1* is demonstrated through transgenic *F. vesca* plants [33••]. *FveSOC1-OX* (overexpression) in wild-type *F. vesca* led to increased expression of *FveTFL1* and delayed flowering regardless of daylength. However, the same *FveSOC1-OX* transgene failed to repress flowering in the *tfl1* mutant background, suggesting that the inhibitory effect of *FveSOC1* on flowering is via *FveTFL1*. In contrast, the *FveSOC1-OX* transgene was shown to promote runner formation independently of photoperiod, and the effect was mediated by GA biosynthesis as GA biosynthesis inhibitor Pro-Ca completely inhibits stolon formation in *FveSOC1-OX* plants. RNAi silencing of *FveSOC1* confirmed that *FveSOC1* controls and coordinates flowering

Figure 3



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A model summarizing regulation of stolon/runner formation and flowering in the seasonal flowering accessions of diploid strawberry. Under LD, the *CO-FT-SOC1* pathway is induced. The increased expression of *FveSOC1* leads to transcriptional activation of the floral repressor *FveTFL1*, which inhibits flowering. At the same time, LD-induced *FveSOC1* upregulates the transcription of GA biosynthetic genes in AXM, leading to GA accumulation in AXM and degradation of FveRGA1/SRL. This enables the runner to develop. Under SD, the expression of *FveSOC1* is reduced, which leads to reduced transcription of flower repressor gene *FveTFL1*; GA biosynthesis is also reduced and the FveRGA1/SRL actively represses runner formation in AXM. Activation is indicated by arrows and repression by bars. Location of the regulation is indicated by the squared boxes: leaf, AXM, and SAM.

and runnering through a branched pathway in wild-type *F. vesca* [20,33••] (Figure 3).

In perpetual flowering *F. vesca* carrying the *tfl1* mutation, the roles of *FveCO* and *FveFT1* are more extensively investigated. Under LD condition, *FveCO* was shown as an activator of *FveFT1* in leaves [37] and silencing *FveFT1* delayed flowering under LD [36,37]. The *FveCO-FveFT1* module in the perpetual flowering accessions appears to exert opposite effects on flowering/runnering from seasonal flowering (wild-type) accessions. In perpetual flowering accessions, *FveCO-FveFT1* could have evolved a new pathway to promote flowering, or the positive effect of *FveCO-FveFT1* on flowering is unmasked after the strong repressor of flowering *FveTFL1* is mutated. Interestingly, perpetual flowering cultivars of garden strawberry produce very few runners, hindering their commercial adoption [20,38]. This phenomenon is explained as a trade-off regulation between flowering and runnering. When more AXMs, especially those just below the primary inflorescences, are destined to become flowering shoots or branch crowns under conditions that favor flowering, fewer AXMs become available for runner formation. *FaPFRU* (*Perpetual Flowering and Runnering*), a single dominant locus in cultivated strawberry with unknown molecular identity, is involved in this aspect of the trade-off regulation between runner and branch crown [38–40].

Advances in investigations of rhizome development

Relatively little is known about the molecular mechanisms and signaling processes underlying rhizome initiation and development. Several QTL studies take advantage of the genetic hybrids between annual crops such as sorghum and rice and their rhizomatous wild relatives [7,8••]. QTLs that influence the number of axillary buds as well as QTLs that determine whether axillary buds differentiate into tillers or rhizomes were identified. Comparisons of rhizomatousness QTLs and tillering QTLs revealed both shared and unique genetic loci [8••]. Several rhizomatousness QTLs in *Sorghum* reside in chromosomal regions containing homologs of rice genes known to affect tillering and other vegetative branching, such as *SHOOTLESS2*, *TILLERING1*, and the *FLO/LFY* ortholog *RFL* [8••].

Gene expression has been utilized to investigate the roles of signals in the elongation, swelling, and transition stages of rhizome growth and development. GA treatment enhances rhizome elongation in the turfgrass *Poa pratensis* and alters expression levels of genes involved in photosynthesis, energy and amino acid metabolism, and other processes [41]. In species where the rhizome swells and functions as a nutrient storage organ, such as lotus (*N.- nucifera*), hormone signal transduction genes such as *GAI*, *PYL*, and *ARF* are differentially expressed between the elongating rhizomes and the swelling stage rhizomes, indicating roles for GA, ABA, auxin, and other phytohormones in rhizome swelling [4].

Before the developmental transition to produce an aerial shoot, rhizomes in the rhizomatous rice relative *O.- longistaminata* are maintained in the juvenile phase, indicated by their juvenile leaf morphology and high expression of the juvenile phase regulator miR156 [1••,42••]. To produce an aerial shoot, the rhizome tip in *O. longistaminata* bends upward and attains negative gravitropism. Sucrose application to the rhizome inhibits the transition to aerial stem and causes reduced expression of *GA20ox* and *PIN1*, suggesting a role for GA and auxin in rhizome transition [43]. Rhizome development thus includes numerous signaling pathways that influence rhizome morphology.

One unique aspect of rhizome development is the need for mechanical support in order to grow through the soil. The gene *BLADE-ON-PETIOLE* (*BOP*) plays an important role in rhizome tip stiffness in *O. longistaminata*. *O. longistaminata* rhizome leaves have a high sheath-to-blade ratio where the sheath confers stiffness and support for the rhizome. The *bop* mutant produces rhizomes that twist through soil due to a lack of rhizome tip stiffness, in contrast to wild-type rhizomes that have straight growth and a stiff rhizome apex [42••]. Among several phylogenetically distant species, such as the stoloniferous turfgrass *Zoysia matrella* and the rhizomatous dicot *Houttuynia cordata*, *BOP* is highly expressed at the rhizome or stolon apex, suggesting that *BOP* repression of leaf blade growth may be a common feature of rhizome and stolon development [42••]. Additional mutant phenotypes associated with rhizome morphology would greatly enhance current understanding of the molecular mechanisms of rhizome development.

Conclusion

Stoloniferous and rhizomatous plants are of tremendous agricultural and ecological importance and occupy broad taxonomy from ferns to monocots and dicots. Since established models, Arabidopsis, tomato, rice, and maize, are not stoloniferous or rhizomatous, the mechanisms of stolon/rhizome initiation and development are poorly understood. This review aims to highlight the need to expand our understanding of unique developmental traits not covered by model organisms and to provide a comparative view between stolon and rhizome with the hope of encouraging investigations into these highly important and unique plant reproductive traits.

Some of the questions that remain unanswered are, how do plants sense environmental conditions, especially temperature, to regulate stolon/rhizome initiation? As earlier work in potato tuberization illustrated mobile signals in regulating the transition from stolon to swelling tubers in potato [2,3], are similar or different mobile signals produced to regulate the initiation of stolons and rhizomes? Are the signals and regulatory mechanisms of stolon formation conserved among different stoloniferous plants? Further, are the regulatory mechanisms of stolon/rhizome formation conserved between stoloniferous and rhizomatous plants? What controls the gravitropic horizontal growth of stolons and rhizomes?

Diploid strawberry (*F. vesca*) is an emerging model system for investigations into stolon development. We illustrate how different natural accessions, *runnerless* Alpine strawberry and perpetual-flowering accessions contribute greatly to the identification of key factors controlling runnering and flowering. We also highlight the success of employing forward genetic screens and reverse genetics in strawberry. With steady improvements of genomic resources in cultivated strawberry [6,44], the rich collections of octoploid strawberry germplasms can be utilized to identify genes underlying major QTLs for runnering and flowering [39,45]. Future transcriptomic network analysis [46] combined with gene editing technologies [47–49] and marker-assisted breeding [50] will not only elucidate the genetic network underlying stolon formation but also enable breeding new strawberry cultivars of desirable stolon/flower ratios.

Genetically tractable systems in rhizomatous species such as *O. longistaminata* should be further developed to enable comparative studies between stolon and rhizome, which should reveal conserved as well as novel mechanisms for plant vegetative reproduction. Such an understanding will not only improve fundamental knowledge of plant development and evolution but also improve plant clonal propagation, increase plant productivity and survival, and enable the control of invasive plants.

Conflict of interest statement

Nothing declared.

CRediT authorship contribution statement

Lei Guo: Writing - original draft, Visualization. **Madison Plunkert:** Writing - original draft, Investigation. **Xi Luo:** Investigation. **Zhongchi Liu:** Writing - review & editing, Visualization, Supervision.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pbi.2020.10.003.

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- • of special interest
- •• of outstanding interest

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