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Review

Biotechnological Interventions for Reducing the Juvenility in Perennials

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Abstract: During shoot apex development, the plants undergo a very complex transition phase of flowering for successful reproduction, seed/cone setting and fruit development. The conversion of vegetative shoot meristems to floral meristems depends upon numerous endogenous, exogenous factors and flowering genes for the development of floral parts. The perennial crops suffer from the limitation of the innate ability to keep some meristems in the vegetative state for the polycarpic growth habit leading to the long juvenile phase. Conventional breeding approaches viz. selection of early flowering parental lines, flower thinning and grafting are time-consuming requiring more time for the release of a new cultivar which is undesirable for rapid crop improvement. The best way to accelerate the perennial plant breeding improvement programs and to reduce the long juvenile phase is the induction of early flowering through the utilization of biotechnological approaches. The ability to allow the transmission of an early flowering gene to the progeny in a Mendelian fashion is the major advantage of biotechnological interventions. The introgression of early flowering traits from non-commercial germplasm or sexually compatible species to perennial species through the biotechnological aspects will act as a boon for crop improvement in future studies. The present review gives an overview of various flowering genes in perennial crops accompanying the implementation of biotechnological approaches including overexpression studies, RNA interference, Virus-induced flowering and CRISPR-Cas approaches that will help in reducing the period for induction of flowering in perennial crops.

Keywords: perennial; early flowering; biotechnological approaches; juvenile; transition phase

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1. Introduction

Perennial agriculture including field crops, vines, conifers and trees holds promise in the present era due to its ability to reproduce more grains, seeds/cones, fruits and biomass. Generally, the plant tends to undergo a vegetative and reproductive series of phase transitions after embryogenesis to complete its life cycle [1,2]. Among these series of phase transitions, the plant has to follow the complex transition phase of flowering during the shoot apex development. The core of the plant developmental process and reproductive success resides in complex flowering mechanisms for proper flower development from flower initiation to the formation of floral organs including sepals, petals, stamens and carpels for fruits and seeds/cones setting in angiosperms [3,4]. The major importance of flowering in plants is its participation in reproduction which mediates the joining of the sperm contained within pollen with the ovules present in the ovary. Flowering also plays a vital role in pollination for the production of nectar to attract pollinators for a successful reproduction process [5].

Besides these advantages, the perennial fruit crops suffer from the major limitation of irregular bearing, bud dormancy and long juvenile phase. The major hindrance in perennial crop species is the characteristic feature of retaining some meristems in the vegetative state leading to the long juvenile phase [6]. Late-flowering tend to initiate basal branching rather

than axillary flowering [7]. Perennial crops have various disadvantages. Recently, Sharma et al. [8] reviewed the detailed information on irregular bearing in perennial fruit crops and the impact of physiological, biochemical, genetic and environmental factors. Based on phyto-gerontology of perennial fruit crops, two major multi-annual reproductive strategies defined alternate bearing phenomenon, i.e., (1) in one-year heavy fruit load ('On' crop), and (2) in the succeeding year low fruit load ('Off' crop). The alternate bearing phenomenon among perennial fruit crops depends upon three important factors i.e., (i) reproductive and vegetative organs implying the site of the flowering competition, (ii) differential nutrients amounts during the 'Off' year and (iii) endogenous phyto-hormonal control [8]. The bud dormancy processes in fruit tree species have also been reviewed by Beauvieux et al. [9] including hormonal signaling, the role of the plasma membrane, carbohydrate metabolism, mitochondrial respiration and oxidative stress.

The juvenility is the incompetency towards flower production and ultimately fruit production. The induction of early flowers is essential for accelerating the fruit crop improvement programme that will result in the reduction of the long juvenility phase followed by efficient fruit production. The early flowering induction in the perennial crops is required to overcome the state of innate long juvenile phase as it is the major impediment to transferring the desirable traits into the elite cultivars, hence, de-accelerating the perennial plant breeding programmes [10]. The long generation time is the hindrance in the dissection using molecular approaches in the perennial crops [3]. The perennial crops tend to exhibit a slow breeding cycle, longer reproductive cycle and high degree of heterozygosity posing difficulties in plant breeding programmes [11,12]. Besides being a slow and arduous process, it is an expensive process due to the requirement of 10 to 20 years for the release of a new cultivar in perennial tree species [11]. The generation of early flowering is a promising strategy to escape the drought conditions for the production of advanced drought-adapted wheat cultivars [13]. The detailed knowledge to understand the early flowering system can reveal the genetics of traits along with the transfer of traits of interest into commercially acceptable germplasm [11]. The use of early flowering plants proved to be beneficial for gene introgression, quantitative trait loci and pyramiding of several genes of interest in a specific pre-breeding line in a limited period of time [14]. In this way, induced early flowering results in the quick screening of species, saving greenhouse space and labor that will boost the selection of new varieties leading to the development of efficient breeding programmes at a lower cost [15]. This review aims to provide detailed information about the prevalence of long juvenile phases among perennial crops. It also enlists the various flowering genes in the perennial plants and implementation of biotechnological approaches including overexpression studies, virus-induced flowering, RNA interference and CRISPR-*Cas* (Figure 1) for the induction of early flowering in perennials. In the previous era, flowering genes were identified by Almeida et al. [16] using analysis of mutant combinations and chromosomal duplication studies.

The fundamental feature in the flowering mechanism is the change in the shape of the shoot apical meristem present at the apex of the plant to become an inflorescence meristem [2]. Its mechanism involves the conversion from vegetative shoot meristems to indeterminate inflorescence meristems followed by determinate floral meristems to complete the flowering mechanism [17].

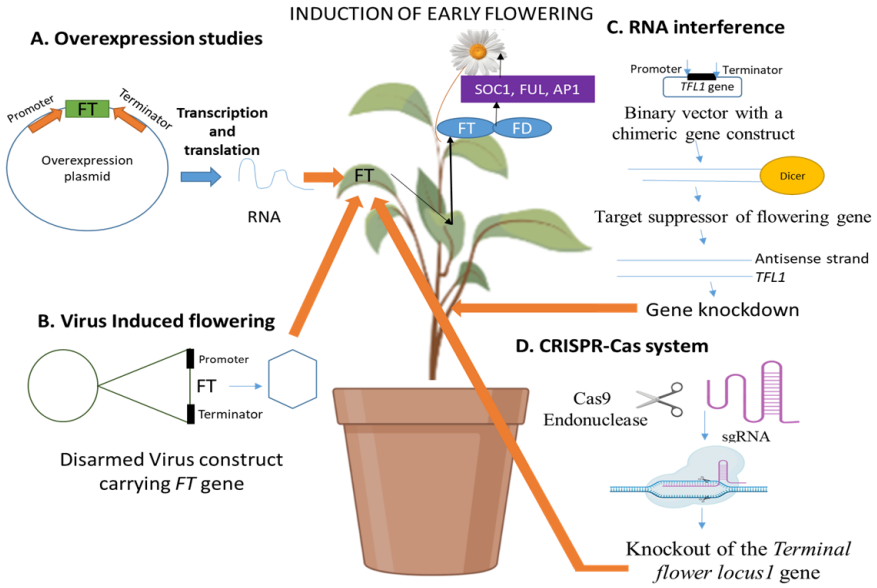

Figure 1. Biotechnological approaches (**A**). Overexpression studies (**B**). Virus-induced flowering (**C**). RNA interference (**D**). CRISPR-Cas system for the reduction of juvenility in perennials.

2. Flowering in Perennials in Comparison to Annual Plants

The perennial plants differ from the annual plants during the flowering reproductive phase [3]. An annual plant follows the conversion of all meristems into floral as well as inflorescence meristems while a perennial plant follows the chance of production of vegetative or a reproductive shoot each year from each meristem [3]. The perennial plants generally have polycarpic or iteroparous life strategies with longer reproductive life with the ability to produce new flowers every year and flowering occurs over multiple years [2,3].

The juvenility stage refers to the period elapsing between seed germination and the first flowering of the seedlings that lack response towards the flower inductive signals in a plant's life cycle [2,18–20]. Although the syntenic relationship between annual *Arabidopsis* and perennial plants showed that genes remain conserved during the evolution of flowering plants, still the flowering patterns of perennial plants differ from annual plants [2,3]. However, the size and longevity make perennial crops more complex than annual plants [1]. The control mechanism of flowering in perennials is different from the flowering in conifers besides similar cultural practices led to the generation of flowering in both tree groups. It has been reported that endogenous gibberellic acid treatment is crucial for flowering in conifers that have a direct morphogenic role in cone bud differentiation [21]. The early flowering in conifers ultimately affects cone setting that has an association with high transcriptional activity of a MADS-Box transcription factor. The upregulation of protein Acr42124_1 was observed in apical shoot samples from cone-setting acrocona plants that encode MADS-box gene family of transcription factors [22].

The perennial plants initiate flowering after the complete development of axillary vegetative shoots and sufficient biomass which is the major requirement for flowering [1]. The floral and inflorescence reversion mechanism involves switching back to vegetative development from the reproductive phase maintain perennial behavior [23]. Flower induction is quantitative in adult fruit trees but it is qualitative in annual/biennial plants [24]. The involvement of the regulation of numerous flowering genes along with its transport through numerous genetic pathways through interactions between external and internal factors makes flowering a complex mechanism [24]. Complex perennial flowering cannot be described based on a single trait conferring flowering behavior [2]. It has been reported that the flowering time variation under stabilizing selection depends upon the complex set of trade-offs involving flowering time in plant species [25]. The evolutionary genetics involving the complex nature of gene interactions and pleiotropy specifically impose on adaptive evolution in flowering plants.

3. Advantages of Induction of Early Flowering

In the past era, the number of researchers shortened the juvenile period through a variety of techniques through increasing seedling growth, artificially inducing multiple dormancy cycles per year, and grafting on particular rootstocks, girdling seedlings and growth regulators [26–28]. The major advantage of the implementation of induction of early flowering in perennial crops is the high-speed breeding [11,29], production of disease-free crops [10], and rapid development of transgenics and functional genomics studies [30]. It has been estimated that during the dormant state of the tree, extreme cold exposure has the chance to kill buds and intermittent warming periods process flower buds to be more susceptible to winter damage before growth resumes in spring. Under these conditions, the emergence of flowers can emerge too early in the spring for the survival of stress under adverse conditions [31]. Flachowsky et al. [29] provided the first report for the development of a transgenic early flowering-based apple breeding programme coupled with marker-assisted selection conferring fire blight resistance in apples. The reduction in the time of the juvenile period is the major achievement in the introgression of desirable traits from wild species into pre-breeding material [29]. The use of rapid cycle breeding is effective in backcross plant-based breeding programs that employ the rapid introgression of desirable early flowering traits from non-commercial or wild-type germplasm into a commercial germplasm background [11,30]. It was observed that by utilization of early flowering mutant lines transformation efficiency enhanced from 18.6% to 29.6% in citrus species. The *FT* gene cloned from sweet cherry (*Prunus avium* L.) also promotes flowering in a winter-annual *Arabidopsis* accession that resulted in the development of transgenic plants with early-flowering phenotype without the requirement of cold treatment [32]. Schlathölter et al. [10] developed an advanced fire blight-resistant apple carrying the fire blight resistance gene using the early flowering transgene and fire blight resistance line of apple.

4. Difficulties Associated with Conventional Approaches to Induce Early Flowering in Perennials

The choice of early flowering parents, favorable cultural practices like flower thinning and grafting led to the shortening of the juvenile period in the past era [26]. A longer growing season also can reduce the longer juvenile period [33–35]. Since long ago, selection favors early flowering plants which is a major force during evolution [36].

The occurrence of a long maturation period is the main reason for complicating the genetic improvement in perennial plants [37,38]. Hence, it is important to accelerate flowering through the reduction of the juvenile phase of plants [19]. Earlier, researchers opted for time-consuming conventional breeding approaches to overcome these difficulties. The lack of synchronized flowering of desired genotypes makes conventional breeding a difficult approach in long juvenile-based plant species [39]. Traditional mutagenesis imposes limitations due to the production of undesirable knockout mutations [40]. Moreover, the conventional approach is a time-consuming process that has the requirement of screening plant material at a large scale which is a tedious task, requires a large area for planting is also a limiting factor in genetics studies [15]. Therefore, nowadays, researchers are utilizing novel biotechnological approaches at a large scale to circumvent the harsh stresses leading to the production of reproductive meristems to initiate early flowering to harness the yield for crop improvement.

5. Factors and Genes Associated with Flowering

Majorly, the meristems, circadian clock and mobile flowering signal *florigen* gene *FLOWERING LOCUS T* (*FT*) play a vital role in carrying transitioning from the vegetative to the reproductive stage [3,41,42]. The floral pathway integrators include *LEAFY* (*LFY*) and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) and floral meristem identity genes, such as *APETALA1* (*AP1*), *FRUITFUL* (*FUL*), *CAULIFLOWER* (*CAL*), *LFY* and *SEPALLATA4* (*SEP4*) are crucial for flower development [3]. The floral induction also depends upon climate, shoot age, bud position and crop load of the plant species [39]. The

floral-pathway genes are responsible for floral bud development resulting in flowering and fruiting within the first year of growth [19,40,41]. The MADS-box genes in a non-flowering seed plant i.e., conifers and genes corresponding to three different deficiens-agamous-like (dal) genes, *dal1*, *dal2* and *dal3*, the spruce genes constituting a second sequence element conserved among angiosperm genes, the K box present downstream to the MADS-box genes are vital for flowering in conifer species. The flowering genes in conifers i.e., *dal1* related to *agl2*, *agl4* and *agl6* from *Arabidopsis thaliana*, and show expression in vegetative as well as reproductive shoots on the adult spruce tree. Secondly, *dal2* is sister to angiosperm genes crucial for controlling the sexual organs, and identity and showing expression only in the developing male and female strobili. The third gene, *dal3* is related to the vegetatively expressed tomato gene *tm3* and show transcription in both vegetative and reproductive shoots [43]. The floral induction also depends upon climate, shoot age, bud position and crop load of the plant species [44]. The floral-pathway genes are responsible for floral bud development resulting in flowering and fruiting within the first year of growth [45]. The circadian regulatory *CONSTANS* (*CO*) gene triggers the expression of the *FT* gene in plants [46–48]. The *FT* gene is majorly expressed during the floral induction period whereas *LFY* and *SEP* respond during the blooming season [49]. The coordination of all these genes responds to multiple flowering signals conferring flowering in plants in a systemic way.

5.1. Flowering genes in Perennials in Response to Exogenous and Endogenous Factors

The developmental switch from the vegetative phase to the reproductive phase includes exogenous and endogenous factors. Both cues include day length, temperature, developmental stage and floral gene activities to initiate flower development [3]. Khan et al. [1] extensively reviewed the role of temperature, day length, gibberellins (GA) signaling and aging in perennial plants. The major environmental cues include temperature, photoperiod and stress conditions (e.g., water deficit and salinity) that have the potential to modulate the flowering responses [50,51]. The five major flowering genetic pathways include environmental induction through photoperiod, vernalization, gibberellins, autonomous floral initiation and aging to enhance flowering in plants [1,52]. All these cues are able to complete the flowering mechanism through numerous flowering genes.

Garner and Allard [53] first demonstrated the effect of the day length on the flowering initiation. Generally, the plants show flowering under both short (*Oryza sativa* L.) and long-day conditions (*Arabidopsis thaliana* L.) [54]. The tropical, subtropical and temperate fruit crops have the requirement of different periods of light and dark periods for flowering [55]. The homologs of *CO* and *FT* (*FT1* and *FT2*) are involved in day-length regulation and have been identified from poplar species, *Populus trichocarpa* L. and *Populus deltoides* L. [56,57]. *CRYPTOCHROME2/FHA* (*CRY2*), *GIGANTEA* (*GI*), *FT*, *CO* and *FLOWERING WAGENINGEN* (*FWA*) have a major role in the regulation of photoperiodic pathway [18,58,59]. Perennials tend to show perpetual flowering (ever bearers) under favorable environmental conditions [2]. *PERPETUAL FLOWERING1* (*PEP1*) is an ortholog of the *FLC* gene involved in vernalization in the perennial species [60]. The genes *LUMINIDEPENDENS* (*LD*), *FLOWERING TIME CONTROL PROTEIN FCA* (*FCA*), *FLOWERING TIME CONTROL PROTEIN FY* (*FY*), *FLOWERING TIME CONTROL PROTEIN FPA* (*FPA*), *FLOWERING LOCUS D* (*FLD*), *HOMOLOGUE OF THE MAMMALIAN RETINOBLASTOMA-ASSOCIATED PROTEIN* (*FVE*), *FLOWERING LOCUS K* (*FLK*) and *RELATIVE OF EARLY FLOWERING 6* (*REF6*) are involved in autonomous pathways [1]. The microRNAs (miR156 and miR172) are involved in aging in perennial crops to maintain the juvenile-mature phase transition [1]. The overexpression of *JcmiR172a* is essential for early flowering, abnormal flowers and altered leaf morphology in transgenic *Arabidopsis thaliana* and *Jatropha curcas* [61]. The plant growth regulator paclobutrazol has the potential to increase the percentage of dry matter allocation in flower buds before the shoot growth that initiates the early flowering in 'Songold' plum [62].

The endogenous substance GA is the inhibitor of floral meristem production [1]. Contrastingly, the GA levels are critical for flower induction and floral organ determination as well as for fruit initiation, development and quality [63–69]. The gibberellin F-box protein,

PslSLY1 is specifically involved in plum fruit development. The nitrogen source for developing flowers is crucial for the early stages of leaf, flower and fruitlet metabolism [70]. The GA has the potential to control flowering to limit the biennial bearing in citrus [3].

The exogenous substances namely cyanogenic glucosides, hydrogen cyanamide and hydrogen peroxide are also vital for inducing early flowering in plants. The turnover of cyanogenic glucosides released during plant defense mechanism in almond and sweet cherry control flower development in *Prunus* species [71]. The treatment of hydrogen cyanamide helps break bud dormancy and promote flowering in perennial deciduous blueberry fruit trees. Hydrogen peroxide also has the potential to break bud dormancy in Japanese pear (*Pyrus pyrifolia Nakai*) [72]. The homologs *FT1* and *FT2* coordinate between vegetative and reproductive growth cycles in woody perennial trees [73,74]. Hence, the coordination between exogenous and endogenous factors confer flowering in perennial plants.

5.2. Various Flowering Genes in Perennial Plants

The production of leaves led to the development of secondary shoot meristems followed by flower meristem formation conferred by a number of several flowering genes [75]. It has been reported that some flowering key genes are preserved in perennial fruit species [76–80]. The genes *FT*, *LFY*, *PISTILLATA* (*PI*), *FT-LIKE* and *AP1-LIKE* (*APETALA1*) are vital for floral meristem identity and floral morphogenesis in pineapple [4,81,82]. *LFY homolog*, *VFL* for flower initiation and *AP1* homolog (*VAP1*) for flower meristem involved in the flower formation in grapevine [83,84]. The movement of the *FT* gene in grafting also has the potential to control flowering in citrus [3]. *AP1* act as a potential marker gene for floral initiation in strawberry [85].

The temperature-related gene *ZjPIF4* increased during the early stages of flowering responsible for floral initiation in the short juvenile phase and fast flower bud differentiation in *Ziziphus jujube* L. (Chinese jujube) perennial fruit plant. The *ZjPHY* family comprising *ZjPIF4*, *ZjFT* and *ZjCO5* is generally involved in the regulatory network of flowering in *Chinese jujube* [86]. The Dormancy-Associated *MADS-Box* genes including *PavDAM1/5* and *PavSOC1* are involved in the flower development in sweet cherries under winter conditions [4]. *MADS*-box gene family members including *AcAGL6* and *AcFUL1* were mainly expressed in sepals and petals in pineapple revealed through transcriptome analysis [87]. The gene *AcSBT1.8* is responsible for the regulation of petal development in pineapple [88]. *FT* genes or orthologues of a *MADS*-box gene known as *FRUITFULL* (*FUL*) are majorly involved in early flowering. The apple *FT2* gene regulates both fruit development and vegetative growth [74]. *Dimocarpus longan FLOWERING LOCUS T1* (*DlFT1)* is a flowering promoter while *DlFT2* acts as a flowering inhibitor [89]. The present review focuses on the induction of early flowering in perennial fruit crops through biotechnological approaches. The knowledge of flowering genes in perennial crops and the implementation of biotechnological approaches has the potential to dissect the complex flowering mechanism in perennial crops. The complex network of numerous flowering genes e.g., miRNA156, which is produced in reponse to plant aging and in turn downregulates the expression of *SPL* (*SQUAMOSA PROMOTER BINDING-LIKE*) transcription factors [90]; i.e., *SPL3 SPL4* and *SPL*5 [91] downregulating expression of floral meristem identity genes (*AP1* and *LFY*). miRNA 169 is involved in regulating flowering [92] and is produced in response to various abiotic stresses like under drought and cold stress [93], which reduces the expression of *FLC* target genes such as *FT* and *LFY* [94]. Also, *RAV* (Related to ABI3 and VP1) family of transcription factors has two DNA binding domains i.e., AP2 and B3 [95] which downregulates the expression of *AP1* and *LFY*. In response to photoperiod and autonomous pathway, *Agamous-like* 24 (*AGL24*) transcription factor is produced which acts together with *SOC1* (*SUPPRESSOR OF CONSTANS1*) and activates *CONSTANS* (*CO*), hence, activating floral integrator gene, *FT* [96], which forms a complex with *bZIP* transcription factor *FD* [97] resulting in flowering in plants. Some of these genes and their roles in the initiation of flowering are shown in Figure 2.

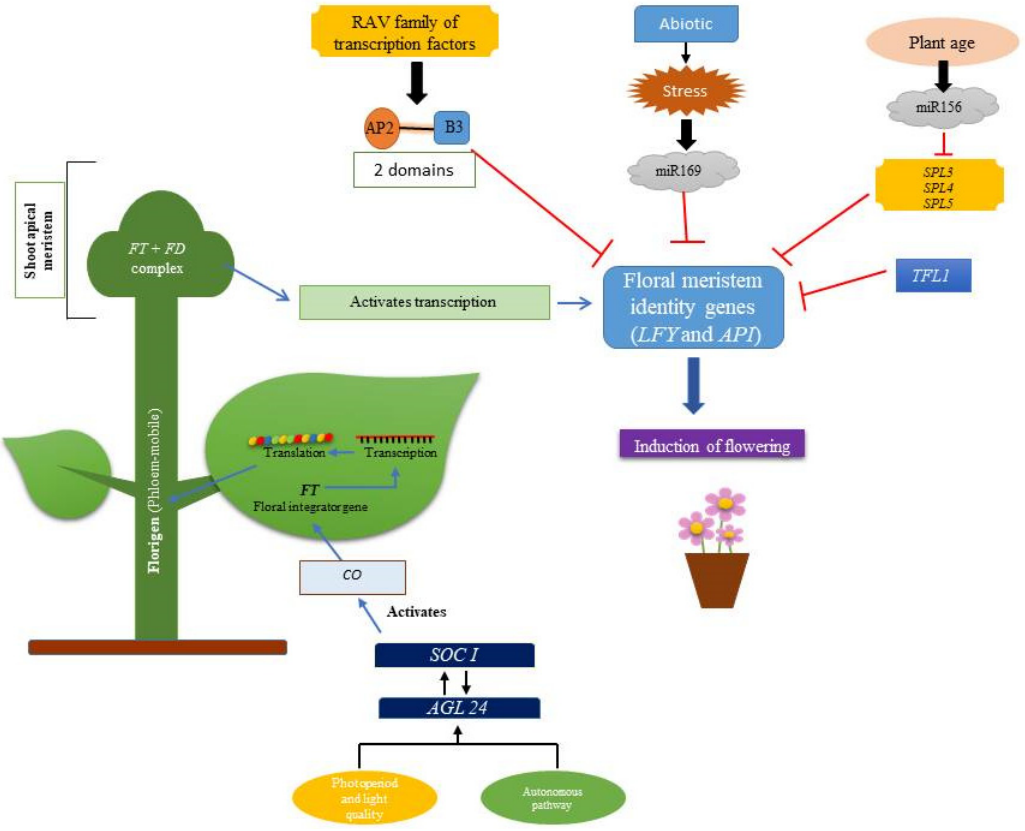

Figure 2. Various genes involved in regulation of flowering in plants [***RAV***, **R**elated transcription factors to ***AP1*** and ***VP1***; stress and age induced microRNAs formed (miRNA169 and miRNA156, respectively) are involved in transcription repression of floral meristem identity genes; i.e., ***LFY*** and ***AP1*** genes whereas ***Agamous like 24*** (MADS box transcription factor) interacts with ***SOC1*** (Suppressor of overexpression of ***CONSTANS***) and activates ***CO1*** (***CONSTANS1***) gene resulting in activation of Floral integrator gene, ***FT***, which interacts with bZIP transcription factor, ***FD***, hence, expressing floral meristem identity genes resulting in flowering].

6. Role of Biotechnology in the Induction of Early Flowering in Perennial Plants

The breakthrough discovery of biotechnological-based DNA sequencing eased the complex research on the number of perennial species in the field of plant sciences. Several flowering genes have been isolated from perennial plants through biotechnological interventions in apples [98–101], citrus [102–104], grapes [105–107] and eucalyptus [108–110] with the advent of DNA sequencing. The advent of biotechnological applications depends upon various strategies i.e., molecular approaches, plant tissue culture, genetic transformation, RNAi, genome editing etc. The molecular methods employ the prediction of color, shelf-life behavior, taste, texture, and nutrition qualities by utilizing marker genes before fruit bearing of a tree. The advanced genetic transformation technologies result in the shortening of juvenile phases of trees, improvement of biotic stress resistance, and phytoremediation among perennial trees [111]. The major plant tissue culture methods i.e micropropagation, embryo culture, somaclonal variations, protoplast and anther cultures are vital for crop enhancement applications. The Genetic Transformation in woody perennials trees has been studied by Pena and Seguin [111]. Biolistic and *Agrobacterium*-mediated transformation techniques have led to the development of fruit crops i.e., Papaya, apple, plum, and pineapple with genetically modified features, that have acquired regulatory permission for pursuing commercialization in the world. We, hereby, describe the various biotechnological approaches including overexpression studies, virus-induced flowering, RNA interference and CRISPR-Cas approaches for induction of early flowering in perennial plants.

6.1. Overexpression Studies

The foremost biotechnological approach includes the constitutive and ectopic overexpression studies of the flowering genes which led to the early flowering by reducing the juvenile period of perennial plants (Table 1). The overexpression studies employ the use of genetic transformation methods such as *Agrobacterium*-mediated gene transfer with the target flowering gene driven by the constitutive Cauliflower mosaic virus 35S-promoter leading to the expression and integration of desired genes in the transformants followed by the assessment through molecular approaches like polymerase chain reaction (PCR), quantitative real-time PCR and Southern blotting.

The constitutive expression of *LFY* and *AP1* flower meristem genes led to the reduction of the generation time of perennials including hybrid aspen and citrus relatives [99,112,113]. The constitutive overexpression of the *Arabidopsis AP1* gene caused the early flowering of tomatoes and silver birch [114,115]. Early-flowering in transgenic *J. curcas* is achieved through the overexpression of the *JcFT* (*SUC2*:*JcFT*) flowering gene [116]. The ectopic expression of *FT* homolog from citrus resulted in the early flowering of trifoliate orange (*Poncirus trifoliata* L. Raf.) and beach rose (*Rosa rugosa* L.) [104,117]. Simultaneously, the constitutive expression of Citrus FT (CiFT) also induced early flowering leading to normal fruit production with viable seeds in trifoliate oranges [101]. The overexpressed apple FT gene was found to induce early flowering in apple and poplar plants [118]. The overexpression of FT1 from Populus trichocarpa or FT2 from Populus deltoides- male poplar hybrid *P. tremula* × *P. tremuloides* resulted in early flowering [14,57]. The transgenic apple overexpressing MdFT1 showed an early flowering phenotype [119]. Along with FT and AP flowering genes, overexpressed basic helix–loop–helix transcription factor gene, SlbHLH22 also induced early flowering and fruit ripening in tomatoes [112]. It has been reported that the overexpression of CO-like genes induced a graft transmissible phloem mobile FT signal to accelerate flowering [20,120]. It has also been observed that transgenic plants showed early flowering phenotypes without altering the normal plant physiology [118]. Therefore, these studies hold promise in attaining the potential value of overexpressed genes in genetic engineering to shorten the juvenile phase in perennial plant species to regulate the flowering process. These studies have control on flowering pathways i.e vernalization, photoperiod, gibberellin, autonomous and the ambient temperature that are involved in flowering regulation.

Table 1. Overexpression studies for the induction of early flowering in perennials.

Plant	Family	Plant Material/Variety	Genes Overexpressed	Original Flowering Occurred after (Juvenile Phase)	Promoter	Vector(s)	Molecular Analysis	Flowering Time Reduced to	Reference(s)
Jatropha (*Jatropha curcas*)	*Euphorbiaceae*	Seedlings	*AGAMOUS homologue gene*	~34.8 days	CaMV35S	35S:JcAG plant over-expression vector, donor vector was pDNOR223 (Spec +) and the destination vector pEarleyGate 100	RNA expression analysis	20–27 days	[87]
Strawberry (*Fragariaananassa*)	Rosaceae	Ruegen	*FvWRKY71*	33 days	FvFUL, FvSEP1, FvAGL42, FvLFY, and FvFPF1, FT	pGBT9, pBD-FvWRKY71, p35S::FvWRKY71 overexpression vector, pRI101-GFP, pAD-FvWRKY71, pAbAi, pGreenII0800-LUC	RNA expression analysis, Yeast one hybrid assay, Dual luciferase reporter system	19 days	[121]
Tomato (*Solanum lycopersicum*)	Solanaceae	Micro-Tom and transgenic lines	*Basic helix–loop–helix transcription factor gene, SlbHLH22*	29 days	CaMV35S	K303 expression vector	Gene transformation, RNA expression analysis	8-10 days earlier than the wild plant	[122]
Strawberry (*Fragaria ananassa*)	Rosaceae	Tudla	*EjLFY-1, a LEAFY (LFY) homolog of loquat (Eriobotrya japonica Lindl.)*	164 days	CaMV35S	pBI121	Polymerase Chain reaction (PCR), quantitative real-time PCR (qRT-PCR) and Southern blotting	23 and 41 days	[82]
Cassava (*Manihot esculenta*)	*Euphorbiaceae*	60444	*Arabidopsis FTgene*	120 days	CaMV35S, alcohol dehydrogenase I	pDONR207	RNA expression analysis	30 days	[123]
Physic nut (*Jatropha curcas* L.)	*Euphorbiaceae*	Wild type *Arabidopsis thaliana* ecotype Columbia (Col-0), and transgenic lines	*FT homolog isolated from Jatropha (JcFT)*	~34.8 days	CaMV 35S and Suc2 promoter	35S::JcFT overexpression vector	Cloning, sequencing, RNA expression analysis	8–14 days	[116]
Apple (*Malus* · *domestic* Borkh.)	Rosaceae	'JM2' (Malus prunifolia (Wild.) Borkh. 'Seishi'×M. pumila Mill. var. paradisiaca Schneid. 'M9')	*Arabidopsis FT gene*	>10 years	rolC, nopaline synthase, CaMV35S	pSM35S, pSMrolC, pSMAK 251	RNA expression analysis	~1 year	[124]
Beach *rose* (Rugose rose)	Rosaceae	Bao White	*FT homolog from Prunus mume*	>3 years	CaMV35S	pMOG22	qRT-PCR	~1 month	[117]
Silver birch (*Betula platyphylla* × *Betula pendula*)	Betulaceae	Non transgenic and transgenic plants	*AP1*	10–15 years	CaMV35S	pROKII-AP1	qRT-PCR	~1 year	[125]
Plum (*Prunus domestica*)	Rosaceae	Bluebyrd plum	*Poplar FT1*	3 to 7 years	CaMV35S	FT transformation vector	RNA expression analysis	1 to 10 months	[126]
Poplar *(Populus)*	Salicaceae	Pinova, Discovery x Prima, *Populus tremula* L. clone W52	*Apple FT gene*	22 days	CaMV35S, symporter gene promoter	p9N-35S, p9N-Suc2	*A. tumefaciens*-mediated floral dip method	4–6 days	[118]

Table 1. *Cont.*

Plant	Family	Plant Material/Variety	Genes Overexpressed	Original Flowering Occurred after (Juvenile Phase)	Promoter	Vector(s)	Molecular Analysis	Flowering Time Reduced to	Reference(s)
Poplar (*Populus tremula* L.)	Salicaceae	Aspen [*P. tremula* L.; German clones W52 and Brauna11, from Wedesbuettel (Tapiau, Russia) and Kamenz (Saxony, Germany)	*Birch FRUITFULL-like MADS-box gene BpMADS4*	40 years	CaMV35S and nopaline synthase	pAKE1	Southern and Northern blotting	7–10 years	[127]
Apple (*Malus domestic* Borkh.)	Rosaceae	Pinova	*BpMADS4 from silver birch (Betula pendula Roth.)*	>10 years	CaMV35	pUC18 pHTT602	qRT-PCR	3–4 months	[14]
Poplar (*Populus*)	Salicaceae	Hybrid aspen *Populus tremula* x *tremuloides*, clone T89 and clonal lines of European aspen trees (*Populus tremula*)	*FT1* from *Populus trichocarpa* or *FT2 from Populus deltoids*	4 weeks	CaMV35S, cell–specific, shoot apical meristem, heat shock–inducible	pBI121, pBI101, pGEM-T Easy	PCR-based genome walking, rapid amplification of cDNA ends	20 years	[57]
Trifoliate Orange (*Poncirus trifoliata* L. Raf.)	Rutaceae	Trifoliate orange (*Poncirus trifoliata* L. Raf.), 'Kiyomi' tangor (*C. unshiu* Marc. · sinensis Osbeck), sour orange (*C. aurantium* L.), and rough lemon (*C. jambhiri* Lush.)	*Citrus FT Homolog*	16–24 weeks	CaMV35S	pCGN1547	Northern and southern blotting	12 weeks	[104]
Tomato (*Solanum lycopersicum*)	Solanaceae	p73	*Arabidopsis APETALA1 (AP1) gene*	Flowering at 11 vegetative nodes	CaMV35S	pROKII	PCR analysis	Flowering at 6 vegetative nodes	[106]
Arabidopsis (*Arabidopsis thaliana*)	Brassicaceae	Apple (*Malus domestica* var. Jonathan)	*MdMADS5*, an *AP1-like gene* of apple	9 weeks	CaMV35S and nopaline synthase	pSMAK251, pAM563, pSMDAD1.1+, pUMDAP1.2+, pUC19	Reverse Transcription (RT-PCR)	5–10 days	[128]
Citrus (*Citrus* spp.)	Rutaceae	Carrizo citrange, a hybrid (*Citrus sinensis* L. Osbeck × *Poncirus trifoliata* L. Raf.)	*Arabidopsis LFY and AP1*	6 and 20 years	CaMV35S	r pROK II, T-DNA	PCR analysis	1 year	[107]

6.2. Virus-Induced Flowering

At present, the researchers are targeting the flowering gene of interest through an approach that employs the use of a virus vector for early flowering known as virus-induced flowering (VIF). The basic idea of using viral vectors is it's being a quick system for the delivery of proteins in plants excluding the need for transformation and regeneration techniques for the production of transgenic plants [15]. The virus vectors have been extensively used for the delivery of flowering homologs to different perennial plants to induce early and precocious flowering (Table 2). Its mechanism involves the direct delivery of the target flowering gene in the host plants without any viral symptoms [39]. In this method, plant genomic DNA is not being transformed and the infected transgenic virus is rarely carried to the next progeny of the plants [129]. Velazquez et al. [15] reported that there is no integration of viral vector with a negligible chance of recombination with the plant genome, pollen, or vector transmission but only a low rate seed transmission, therefore, a widely employed method for induction of early flowering in perennial plants.

Precocious flowering is a considerable character to reduce the vegetative phase to obtain early fruiting [20]. The delivery of *FT* protein with the use of a virus vector resulted in the termination of the vegetative growth and induction of early flowering in plants [15]. The use of viruses to deliver sequences to promote flowering devoid of the risk of somaclonal variations as viruses perpetuate throughout the whole plant system [39,130]. Researchers have mainly used the apple latent spherical virus vector (ALSV) because of not inducing any viral symptoms in most of the host plants. After transformation, the integrated virus has the possibility to remove from infected apple and pear species with simple heat treatment [131]. The citrus leaf blotch virus-based vector (CLBV) also has the potential to induce early flowering without causing any alteration to the plant architecture, leaf, flower and fruit morphology [15]. Therefore, in the future, the researchers should focus on the development of "regulation friendly" vectors, strains and additionally, basic research on strain specificity to enhance the specificity of virus-induced flowering.

Table 2. Virus-induced flowering in perennials.

Plant	Family	Plant Material	Virus Vector	Target	Molecular Analysis	Reduction in Juvenile Phase	Reference(s)
Grapevine (*Vitis vinifera*)	Vitaceae	*Vitis* spp. 'Koshu', V. vinifera 'Neo Muscat'	Apple latent spherical virus	*Arabidopsis thaliana* Flowering locus T	qRT-PCR, In situ hybridization	20–30 days	[131]
Strawberry (*Fragaria ananassa*)	Rosaceae	Yotsuboshi, Dover	Apple latent spherical virus	*Arabidopsis thaliana* Flowering locus T	Reverse transcription loop-mediated isothermal amplification, In situ hybridization	2 months	[129]
Citrus (*Citrus* spp.)	Rutaceae	*C. excels*	Citrus leaf blotch virus	*Arabidopsis thaliana* Flowering locus T	RT-PCR and qRT-PCR	4–6 months	[15]
Pear (*Pyrus communis* L.)	Rosaceae	Apple 'Ourin,' Pear 'La France,' and 'Bartlett,' and Japanese pear 'Shinkou	Apple latent spherical virus	*PcTFL1-1* gene	qRT-PCR	2 months	[132]
Apple (*Malus · domestica* Borkh.)	Rosaceae	*Chenopodium quinoa*	Apple latent spherical virus	*Arabidopsis thaliana* Flowering locus T and *MdTFL1-1*	qRT-PCR	1 year or less	[133]
Apple (*Malus · domestica* Borkh.)	Rosaceae	Fuji', 'Orin' and 'Golden Delicious'	Apple latent spherical virus	*Arabidopsis thaliana* Flowering locus T	Northern blotting, In situ hybridization, qRT-PCR	1.5–2 months	[134]
Apple, Pear and Japanese pear	Rosaceae	Seeds of Apple, Pear, and Japanee pear	Apple latent spherical virus	Apple *TERMINAL FLOWER 1* (*MdTFL1*)	semi-quantitative RT-PCR, Northern blot hybridization, and RT-PCR-Southern blot hybridization	Precocious flowering	[135]

6.3. Gene Silencing through RNA Interference

RNA interference (RNAi) is a gene knockdown mechanism that has been extensively used for crop improvement [136]. It is a natural mechanism for the regulation of gene expression in all higher organisms without any effect on the expression of other plant genes that promises accuracy and precision in crop improvement [136,137]. Researchers have opted for RNAi methods to induce early flowering in perennial fruit crops (Table 3). RNAi induced by double-stranded RNA with the involvement of Dicer or Dicer-like and Argonaute family proteins triggers gene silencing of the target gene of interest [138]. Its mechanism involves the construction of a binary vector with a chimeric gene construct encoding for a hairpin RNA homologous to the coding sequence of the target suppressor of the flowering gene followed by transformation through *Agrobacterium tumefaciens*-mediated transformation [139]. The loss of function of *TERMINAL FLOWER1* (*TFL1*), which is an inhibitor of the *FT* gene conferred early flowering in apples and pears through the RNAi mechanism [37,128,139]. The targeting of the FRIGIDA-like protein 3 (FRL3) mRNA through the use of potato spindle tuber viroid-derived small RNA also achieved early flowering in tomatoes through the RNA interference approach [140]. In *Jatropha curcas*, an orthog of defective in anther dehiscence gene was silenced [141]. Thus, it is a convenient approach for post-transcriptional gene silencing of the anti-flowering gene to reduce juvenility and induce early flowering in perennial plants.

6.4. CRISPR-Cas System

CRISPR-Cas system is one of the best alternative methods to classical plant breeding for crop improvement in the present era [12]. It has the great potential to accelerate flowering in perennials (Table 3). Its mechanism involves the knockout of the suppressor of the flowering gene employing single guide RNA associated with the Cas9 nuclease of the target gene to induce targeted mutagenesis [12]. Charrier et al. [12] were the first to report the use of the CRISPR-Cas9 system for the induction of early flowering in apples and pears. Early flowering in apples (93%) and pears (9%) was observed through CRISPR-Cas based knock out of floral inhibitor *TFL1* gene, a negative regulator of flowering. Varkonyi-Gasic et al. [17] targeted *CENTRORADIALIS*-like genes to convert the long juvenility and axillary flowering into rapid terminal flowering through the CRISPR-Cas approach in kiwifruit. Though limited research for the induction of early flowering has been carried out, therefore, CRISPR-Cas has the capability to create precise editing to overcome the bottleneck of juvenility in numerous perennials in the future.

Table 3. Biotechnological approaches (RNA interference, CRISPR-*Cas*) for the induction of early flowering in perennials.

Plant	Family	Plant Material	Target	Vector	Promoter	Transformation Method/Efficiency	Molecular Analysis	Observations	Reference(s)
RNA Interference									
Jatropha (*Jatropha curcas*)	Euphorbiaceae	Wild type and JcDAD1-RNAi transgenic Jatropha plants	*DEFECTIVE IN ANTHER DEHISCENCE 1 (DAD1)*	JcDAD1-RNAi	CaMV35S	*Agrobacterium tumefaciens*-mediated transformation	qRT-PCR	More and larger flowers with increased fruit number	[142]
Tomato (*Solanum lycopersicum*)	Solanaceae	Rutgers cultivar	*FRIGIDA-like protein 3* (*FRL3*)	Potato spindle tuber viroid derived small RNA	CaMV35S	*Agroinfiltration*	qRT-PCR, 5′ RNA ligase-mediated rapid amplification of cDNA ends and Illumina sequencing	Early flowering at 35 days post inoculation	[132]
Pear (*Pyrus communis* L.)	Rosaceae	Spadona cultivar	*PcTFL1-1* and *PcTFL1-2*	*MdTFL1* RNAi cassette	CaMV35S	*Agrobacterium tumefaciens*-mediated transformation	Southern hybridization and qRT-PCR	Development of a transgenic early flowering pear	[37]
Tomato (*Solanum lycopersicum*)	Solanaceae	Moneymaker, Wild type, Lin5i-1, and Lin5i-15 genotype	*Lycopersicum Invertase5* (*LIN5*)	pART27	CaMV35S	*Agrobacterium tumefaciens*-mediated transformation	qRT-PCR	Altered flower and fruit morphology, displaying increased numbers of petals and sepals per flower	[143]
Apple (*Malus domestica* Borkh.	Rosaceae	Holsteiner Cox' and 'Gala	*MdTFL1*	pHELLSGATE12	CaMV35S	*Agrobacterium tumefaciens*-mediated transformation	Southern hybridization and qRT-PCR	Flowering within 6 months	[139]
Apple (*Malus domestica* Borkh.)	Rosaceae	Orin cultivar	*MdTFL1 like* gene	pSMDTFL1.1	CaMV35S and nopaline synthase gene promoter	*Agrobacterium tumefaciens*-mediated transformation	Southern, northern hybridization and qRT-PCR	Precocious flowering and developed fruit	[128]
CRISPR-*Cas* approach									
Apple (*Malus x domestica* Bork.)	Rosaceae	Gala	*Terminal Flowering 1* (TFL1)	Binary vectors CRISPR-PDS and CRISPR-TFL1.1, pDONR2017-U3gRNA1-U6gRNA2 vector and pDE-CAS9Kr vector	MdU3 or MdU6 promoters, CaMV35S promoter, *A. thaliana* U6 promoter, parsley ubiquitin	93%	PCR and sanger sequencing	Early flowering in apple transgenic lines	[12]
Pear (*Pyrus communis* L.)	Rosaceae	Conference	*TFL1*	-do-	-do-	9%	PCR and Sanger sequencing	Early flowering in pear transgenic lines	[12]
Kiwifruit (*Actinidia chinensis*)	Actinidiaceae	Hort16A' (*A. chinensis* Planch. var. chinensis)	*CENTRORADIALIS-like* genes	pDE-Cas9 (KanR), destination vector pDE-KRS, *35S:GUS* vector	Arabidopsis U6-26 and U6-29 promoters (U6-CEN4), or Arabidopsis U3-b and U3-d promoters (U3-CEN4), CaMV35S promoter	75% and 30% of U6-CEN4 and U3-CEN4	qRT-PCR and Sanger sequencing	Conversion of long juvenility and axillary flowering into rapid terminal flowering	[17]

7. Limitations

Although crop management outside the regular cropping systems has the potential to fulfil the food supplydemand still it suffers from the limitation of low yield in different plants. The production of extended flower development in the transgenic lines led to the reduction of vegetative growth which results in the lack of fruit and seed production [37]. Sritongchuay et al. [143] reported that early induced flower has the requirement of pollinators honey bees in longan (*Dimocarpus longan* Lour.) and also proved that the absence of native pollinators during artificially induced early flowering decreased the crop yield. Although the expression of the *Jatropha curcas AP1* gene resulted in early flowering in *Arabidopsis*, it is not in the case of *Jatropha* l species, therefore, in these cases, the syntenic studies would be beneficial for the identification of genes conferring early flowering in plant species [61].

8. Conclusions and Future Prospects

The early flowering trait in perennials has the potential to enhance the understanding of the complexity and diversity of flowering mechanisms in perennial species. The syntenic studies would help to decipher the flowering gene of interest in the other relative crop species which will ease the molecular understanding of perennial flowering. The attainment of early flowering in perennial plants and from model plants to economically important crops and vice versa would also be helpful in the dissection of many agronomic traits in near future. The prevailing genomic and transcriptomic tools are vital for the understanding of the metabolic and molecular processes involved in floral biology. Wang et al. [144] performed the metabolomic analysis that showed an increase in soluble sugars (fructose, glucose, maltose), organic acids (citric acid, alpha-ketoglutaric, succinic acid) and amino acids (aspartic acid, glutamic acid, phenylalanine), and increase of tricarboxylic acid cycle increase and phenylpropanoid accumulation essential for breaking bud dormancy to promote flowering. This review will scrutinize the floral gene knowledge in perennial species through the thorough study of complex metabolic and molecular regulatory pathways involved in early flowering. The in-depth knowledge of flowering genes will allow the regeneration of plants in a greenhouse with the possibility to grow on a year-round basis. The exploitation of early flowering genes will allow its transmission in progeny hence, accelerating the breeding programme in perennial crops. The introgression of flowering traits from non-commercial germplasm or sexually compatible species is possible through the biotechnological aspects conferring early flowering in perennial crop species through early phenotype selection. The biotechnological approaches hold promise for the induction of early flowering in the development of new varieties across the horticultural sector in the future. The studies on florigen and anti-florigen action will help to explore the plant adaptability feature in the near future. Moreover, the combinatorial approach of genomics and rapid cycle breeding methods will prove to be a powerful tool for accelerating the speed and cost reduction of conventional breeding leading to the improvement in perennial crops [145]. The rapid development of next-generation sequencing technologies and bioinformatics tools capable to complete genome sequencing of numerous perennial fruit crops, thus, provide a starting point to unveil the existing genetic variation and diversity on a genome-wide scale [146] hence, providing milestones for improving the agronomic traits in perennials. The future would be the dissection of genes through functional genomics studies to analyze the genes associated with flower or fruit traits in perennial fruit crops. Although advanced selections with genes of "wild" origin introgressed into the elite cultivar are 4–5 times faster than that of classical breeding but the implementation of biotechnological aspects has the potential to obtain the trait of interest in a faster manner in a limited period of time.

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