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Physiological and Molecular Mechanisms in Fruit Tree Growth and Development

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Abstract: -

Fruit trees are long-lived perennial crops whose productivity depends on the precise coordination of vegetative growth, seasonal dormancy, flowering, fruit set, fruit growth and ripening. These processes are governed by interacting layers of regulation: environmental signals such as temperature, photoperiod, water and light; hormonal and carbohydrate signalling; and transcriptional, post-transcriptional and epigenetic networks. Over the past two decades, genome sequences of apple, peach, pear, citrus and grapevine, together with functional studies of key regulators, have begun to reveal how these layers are integrated. This review synthesises current knowledge on juvenility and phase change, shoot architecture and rootstock effects, the induction and release of bud dormancy, floral induction and alternate bearing, fruit set, fruit growth and source-sink relationships, ripening and quality formation, and responses to abiotic stress. We highlight central regulators including the miR156–SPL module, FT/TFL1 genes, DAM/SVP-type MADS-box factors, ethylene- and ABA-dependent ripening networks, and R2R3-MYB anthocyanin regulators, and discuss emerging tools for genome editing and accelerated breeding. Finally, we identify gaps in knowledge, particularly the need for tissue-specific, multi-omic and field-validated studies in a changing climate.

Keywords: Bud dormancy; epigenetics; juvenility; temperate fruit trees etc.

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Introduction:

Fruit trees such as apple, pear, peach, plum, cherry, citrus, mango and olive supply essential nutrients, fibre and bioactive compounds to human diets and underpin high-value horticultural industries worldwide. Unlike annual crops, they combine long juvenile phases, repeated annual cycles of growth and rest, and a reproductive output that is shaped by the carbohydrate and hormonal history of the whole tree. A decision made by a bud in one season, such as whether to remain vegetative or to differentiate flowers, determines yield in the next, and these decisions are influenced by crop load, climate and management (Goldschmidt 2013). Understanding fruit tree biology at the physiological and molecular level has become more urgent for three reasons. First, warming winters threaten the chilling accumulation that many temperate species require to break dormancy and flower uniformly (Atkinson et al. 2013). Second, breeding is slowed by juvenility that can last several years, so that a single generation cycle may take a decade or more (Hanke et al. 2007). Third, consumers and markets demand consistent fruit size, colour, texture and flavour, all of which arise from developmental programmes that are sensitive to environment and orchard management.

Juvenility, Phase Change and Tree Architecture

The juvenile-to-adult transition

Seedling fruit trees pass through a juvenile phase during which they cannot flower regardless of inductive conditions. In temperate pome and stone fruits this phase typically lasts several years, and it is a major bottleneck in breeding. Phase change in plants is regulated by a conserved temporal mechanism in which the microRNA miR156 is abundant in juvenile tissues and declines with age, relieving repression of SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (*SPL*) transcription factors that promote adult traits and floral competence (Wu and Poethig 2006). Small RNA profiling in apple has revealed conserved and novel miRNAs and tasiRNAs with putative regulatory networks that likely include this module (Xia et al. 2012).

Shoot growth, branching and canopy form

Fruit tree architecture results from the activity of apical and axillary meristems, the formation of long and short shoots, and branch orientation. Architecture affects light interception, fruit quality, pruning requirements and susceptibility to disease, and it has been analysed through quantitative descriptions of growth units, branching and flowering. At the hormonal level, auxin

exported from the shoot apex inhibits axillary bud outgrowth indirectly, while cytokinin promotes it and strigolactones act as additional repressors; integration of these signals, together with sugar availability, determines bud activation (Brewer et al. 2013).

Rootstock influences on scion growth

Grafting is nearly universal in commercial fruit production, and rootstocks regulate scion vigour, precocity, nutrient and water uptake and tolerance to biotic and abiotic stress. Dwarfing apple rootstocks reduce scion growth by modifying hormone transport, carbohydrate allocation and cell growth. Foster et al. (2017) reported that dwarfing rootstocks are associated with an imbalance in carbohydrate allocation and reduced cell growth and metabolism in the scion, consistent with an effect on the transport of growth-regulating signals across the graft union. Rootstock-derived mobile signals, including hormones, small RNAs and proteins, remain an active area of research.

The Seasonal Dormancy Cycle

Terminology and induction of dormancy

Growth cessation and bud set are triggered by shortening days and falling temperature, the relative importance of which varies by species. In poplar, short photoperiod is dominant, whereas in apple and pear, low temperature rather than photoperiod has been shown to control growth cessation and the induction and release of dormancy. Downstream of these cues, ABA accumulation and the closure of plasmodesmata by callose deposition limit cell-to-cell communication in the bud, an ABA-dependent mechanism demonstrated in hybrid aspen (Tylewicz et al. 2018). Reviews of the signals regulating dormancy are provided by Cooke et al. (2012).

Hormones, carbohydrates and bud break

Abscisic acid generally promotes dormancy induction and maintenance, while gibberellins promote its release and subsequent growth. In grapevine, ABA levels decline in buds as dormancy is released, and dormancy-breaking stimuli appear to act by modifying ABA metabolism (Zheng et al. 2015). Once endodormancy has been released, bud break during ecodormancy is controlled by temperature accumulation (forcing), carbohydrate mobilisation, activation of cell-cycle genes and renewed water uptake. Because the forcing requirement and the chilling requirement interact, models of bud break that account for both are needed for predicting phenology under climate change.

Floral Induction and Alternate Bearing

Molecular control of flower induction

Flowering in fruit trees differs from that of annual model plants in that flower induction, initiation and differentiation are often separated in time, with floral primordia formed in the season before anthesis. Floral

induction is influenced by temperature, light, water status, carbohydrate reserves and hormones, and these inputs are integrated through FT-like florigens and TFL1-like repressors. In apple, *MdFT1* and *MdFT2* display distinct expression patterns and promote early flowering in transgenic Arabidopsis, indicating functional diversification of FT genes (Kotoda et al. 2010). The environmental trigger varies among species. In Satsuma mandarin, floral induction is correlated with increased *CiFT* abundance in stems following exposure to low temperature (Nishikawa et al. 2007), while in olive, FT-encoding genes interpret both environmental and internal cues that affect flower induction (Haberman et al. 2017). In temperate Rosaceae, the timing of induction is typically linked to the cessation of shoot growth in summer, when apical meristems are released from vegetative growth and become responsive to floral signals.

Alternate bearing

Alternate (biennial) bearing, in which a heavy crop in one year is followed by a light crop in the next, is a major problem in apple, citrus, olive, pistachio and mango. The classical explanation is that developing fruit, and in particular their seeds, inhibit floral induction in adjacent buds, probably via gibberellins and competition for resources, so that a large crop suppresses flowering for the following season. Recent work in olive suggests that fruit load modulates FT-encoding gene expression in buds (Haberman et al. 2017), providing a molecular link between crop load and floral induction. Practical management, including chemical or manual thinning early in the season, is designed to interrupt this feedback.

Genomics and Biotechnology

Reference genome sequences are now available for apple (Velasco et al. 2010), peach (Verde et al. 2013), pear (Wu et al. 2013), sweet orange (Xu et al. 2013) and grapevine (Jaillon et al. 2007), among others. These resources have enabled the identification of whole-genome duplication events in Rosaceae, mapping of quantitative trait loci for dormancy, fruit quality and disease resistance, and comparative analysis of gene families such as MADS-box, MYB and NAC. Combined with transcriptomic, epigenomic and metabolomic data, they provide a framework for dissecting developmental processes at high resolution. Functional genomics in perennial fruit trees is constrained by long generation times and, for several species, by low transformation efficiency. Strategies to overcome these constraints include the use of early-flowering transgenic lines for rapid breeding cycles and the heterologous expression of flowering genes. Genome editing offers a precise alternative:

CRISPR/Cas9 has been used to generate targeted mutations in apple (Nishitani et al. 2016), establishing proof of concept for editing genes controlling flowering time, dormancy, fruit colour and disease susceptibility. Regulatory frameworks for edited fruit trees differ among countries and will influence the pace of adoption.

Conclusions

Advances in genomics and molecular physiology have transformed understanding of how fruit trees grow, rest, flower and fruit. Conserved regulators of phase change, flowering and dormancy, together with hormonal and epigenetic mechanisms, provide a coherent but still incomplete framework. Closing the remaining gaps, especially in species-specific validation, climate resilience and the integration of molecular data with orchard-scale physiology, will be essential for sustaining fruit production under changing climatic conditions.

References

1. Atkinson CJ, Brennan RM, Jones HG (2013) Declining chilling and its impact on temperate perennial crops. Environ Exp Bot 91:48–62
2. Brewer PB, Koltai H, Beveridge CA (2013) Diverse roles of strigolactones in plant development. Mol Plant 6:18–28
3. Cooke JEK, Eriksson ME, Junttila O (2012) The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. Plant Cell Environ 35:1707–1728
4. Foster TM, McAtee PA, Waite CN, Boldingh HL, McGhie TK (2017) Apple dwarfing rootstocks exhibit an imbalance in carbohydrate allocation and reduced cell growth and metabolism. Hortic Res 4:17009
5. Goldschmidt EE (2013) The evolution of fruit tree productivity: a review. Econ Bot 67:51–62
6. Haberman A, Bakhshian O, Cerezo-Medina S, Paltiel J, Adler C, Ben-Ari G, Mercado JA, Pliego-Alfaro F, Lavee S, Samach A (2017) A possible role for flowering locus T-encoding genes in interpreting environmental and internal cues affecting olive (*Olea europaea* L.) flower induction. Plant Cell Environ 40:1263–1280
7. Hanke MV, Flachowsky H, Peil A, Hättasch C (2007) No flower no fruit-genetic potentials to trigger flowering in fruit trees. Genes Genomes Genomics 1:1–20
8. Jaillon O, Aury JM, Noel B, et al. (2007) The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla. Nature 449:463–467

9. Kotoda N, Hayashi H, Suzuki M, Igarashi M, Hatsuyama Y, Kidou S, Igasaki T, Nishiguchi M, Yano K, Shimizu T, Takahashi S, Iwanami H, Moriya S, Abe K (2010) Molecular characterization of *FLOWERING LOCUS T*-like genes of apple (*Malus* × *domestica* Borkh.). Plant Cell Physiol 51:561–575

10. Nishikawa F, Endo T, Shimada T, Fujii H, Shimizu T, Omura M, Ikoma Y (2007) Increased *CiFT* abundance in the stem correlates with floral induction by low temperature in Satsuma mandarin (*Citrus unshiu* Marc.). J Exp Bot 58:3915–3927

11. Nishitani C, Hirai N, Komori S, Wada M, Okada K, Osakabe K, Yamamoto T, Osakabe Y (2016) Efficient genome editing in apple using a CRISPR/Cas9 system. Sci Rep 6:31481

12. Tylewicz S, Petterle A, Marttila S, Miskolczi P, Azeez A, Singh RK, Immanen J, Mähler N, Hvidsten TR, Eklund DM, Bowman JL, Helariutta Y, Bhalerao RP (2018) Photoperiodic control of seasonal growth is mediated by ABA acting on cell–cell communication. Science 360:212–215

13. Velasco R, Zharkikh A, Affourtit J, et al. (2010) The genome of the domesticated apple (*Malus* × *domestica* Borkh.). Nat Genet 42:833–839

14. Verde I, Abbott AG, Scalabrin S, et al. (2013) The high-quality draft genome of peach (*Prunus persica*) identifies unique patterns of genetic diversity, domestication and genome evolution. Nat Genet 45:487–494

15. Wu G, Poethig RS (2006) Temporal regulation of shoot development in *Arabidopsis thaliana* by miR156 and its target *SPL3*. Development 133:3539–3547

16. Wu J, Wang Z, Shi Z, et al. (2013) The genome of the pear (*Pyrus bretschneideri* Rehd.). Genome Res 23:396–408

17. Xia R, Zhu H, An YQ, Beers EP, Liu Z (2012) Apple miRNAs and tasiRNAs with novel regulatory networks. Genome Biol 13:R47

18. Xu Q, Chen LL, Ruan X, et al. (2013) The draft genome of sweet orange (*Citrus sinensis*). Nat Genet 45:59–66

19. Zheng C, Halaly T, Acheampong AK, Takebayashi Y, Jikumaru Y, Kamiya Y, Or E (2015) Abscisic acid (ABA) regulates grape bud dormancy, and dormancy release stimuli may act through modification of ABA metabolism. J Exp Bot 66:1527–1542