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BREEDING FOR FLOWERING SYNCHRONY IN VEGETABLE CROPS: GENETIC, ENVIRONMENTAL AND MOLECULAR DETERMINANTS OF REPRODUCTIVE COORDINATION

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ABSTRACT:
Flowering synchrony is a critical yet underexplored component of reproductive success in vegetable crops, influencing pollen availability, stigma receptivity, fertilization, fruit set, seed production and harvest uniformity. Unlike conventional flowering-time traits, reproductive synchrony encompasses the temporal coordination of floral initiation, anthesis, sex expression, pollen release and pistil receptivity across flowers, plants and parental genotypes. This review examines the physiological, genetic, environmental and molecular determinants governing flowering synchrony in major vegetable crops, with emphasis on the interactions between genotype, environmental conditions and reproductive processes. The influence of temperature, photoperiod, water availability and other environmental factors on flowering and pollen–stigma coordination is discussed, together with the roles of flowering-time, hormonal and sex-expression regulatory networks. The review further evaluates conventional breeding, quantitative genetics, marker-assisted selection, genomic selection, genome editing and multi-omics approaches for improving reproductive coordination. Advances in precision phenotyping and artificial intelligence are highlighted as emerging tools for quantifying flowering trajectories, reproductive windows and synchrony across breeding populations. Particular emphasis is placed on developing climate-resilient cultivars capable of maintaining stable reproductive coordination under environmental variability. Integrating precision phenotyping with genomics and targeted breeding could establish flowering synchrony as a measurable breeding trait, providing a framework for improving pollination efficiency, reproductive stability and yield in future vegetable production systems.

INTRODUCTION

Flowering represents a critical transition from vegetative to reproductive development and ultimately determines the timing and efficiency of sexual reproduction in flowering plants. In vegetable crops, reproductive success has direct consequences for fruit, pod and seed production and therefore for yield, crop duration and commercial value. However, reproductive success is not determined solely by whether a plant flowers early or late. Rather, it depends on the temporal coordination of several developmental events, including floral initiation, flower opening, pollen maturation and release, stigma receptivity, pollination and fertilization. Successful reproduction therefore requires appropriate temporal coordination among male and female reproductive functions, with pollen availability and pistil receptivity occurring within defined developmental windows (Dresselhaus *et al.* 2016; Irfan *et al.* 2023).

This temporal coordination can be broadly described as flowering or reproductive synchrony, encompassing the overlap of reproductive events within and among plants. At the individual-plant level, synchrony may determine

the extent to which flowers reach anthesis and reproductive maturity within a common period, whereas at the population level it influences the availability of compatible pollen and receptive stigmas. Its importance becomes particularly evident in crops with specialized reproductive systems. In monoecious and sex-variable vegetables such as cucurbits, the timing and pattern of male and female flower production can strongly influence opportunities for pollination and fruit production. In cucurbits, sex expression is regulated by genetic and hormonal pathways and is also influenced by environmental factors such as temperature, light and photoperiod (Li *et al.* 2012; Boualem *et al.* 2015). Similarly, self-incompatible plants require the temporal and spatial coincidence of compatible pollen and receptive stigmas for successful fertilization (Dresselhaus *et al.* 2016). Thus, flowering synchrony extends beyond the conventional measurement of days to first flowering and represents a broader component of reproductive coordination.

The consequences of reproductive desynchronization are particularly important in vegetable production because the period between anthesis, pollination and successful fertilization can be highly sensitive to environmental conditions. Pollen development, pollen viability, anther dehiscence, stigma receptivity, pollen germination and pollen-tube growth can respond differently to environmental cues, potentially narrowing or shifting the effective reproductive window (Zinn *et al.* 2010; Hedhly 2011). Consequently, plants exhibiting similar flowering dates under favourable conditions may differ substantially in reproductive success when exposed to environmental fluctuations. Heat stress, for example, can disrupt several stages of reproductive development, including flowering, gametophyte development, pollen viability and germination, pollination, fertilization and subsequent fruit or seed set (Zinn *et al.* 2010; Mehmood *et al.* 2025). In vegetable crops specifically, high temperature has been associated with impaired fruit set and yield losses, particularly in fruiting vegetables (Bisbis *et al.* 2018). Such effects highlight an important distinction between flowering time and reproductive synchrony: a crop may maintain an apparently desirable flowering date while experiencing poor synchronization between male and female reproductive processes.

Environmental variation further complicates the genetic regulation of flowering and reproductive coordination. Temperature, photoperiod, water availability, light and other environmental signals influence the transition to flowering and subsequent reproductive development, while genotype-dependent responses determine the extent to which these processes are advanced, delayed or disrupted (Song *et al.* 2015)[9,10]. Photoperiodic and circadian mechanisms are particularly important components of flowering-time regulation, allowing plants to integrate day length and time-of-day information into the decision to transition to reproductive development (Song *et al.* 2015). Hormonal pathways, including gibberellin and other phytohormonal networks, further integrate environmental signals with the flowering regulatory network (Conti 2017). Climate change is therefore expected to affect reproductive synchrony not only through shifts in flowering phenology but also through changes in the physiological performance of reproductive organs. Reviews of vegetable crops indicate that changes in temperature, precipitation and other climatic variables can alter crop phenology and productivity, with heat stress particularly affecting fruit set in fruiting vegetables (Bisbis *et al.* 2018). At a broader ecological level, climate-driven changes in plant and pollinator phenology can also modify the temporal relationships required for effective pollination, although the magnitude and direction of these effects vary among species and environments (Hegland *et al.* 2009; Byers 2017; Burkle *et al.* 2013).

From a breeding perspective, these observations suggest that flowering synchrony should not be considered simply as a consequence of flowering time but as a multicomponent quantitative trait influenced by genetic architecture, environmental responsiveness and reproductive physiology. Conventional breeding has traditionally emphasized traits such as days to flowering, earliness, flowering duration, flower number and sex expression. These traits remain important, but individually they provide an incomplete description of reproductive coordination. Two genotypes with comparable flowering dates may differ in pollen viability, stigma receptivity, anthesis timing or male–female overlap and consequently exhibit different levels of fruit or seed set. A more comprehensive breeding framework would therefore consider the temporal relationships among these traits rather than optimizing flowering time in isolation.

Understanding the genetic and molecular basis of this coordination provides opportunities to move from descriptive phenology toward precision breeding for reproductive synchrony. Flowering-time pathways involving photoperiod perception, circadian regulation, hormonal signalling and floral meristem identity interact to regulate the transition to reproductive development (Song *et al.* 2015; Conti 2017; Cho *et al.* 2017). In parallel, pathways controlling sex expression, gametophyte development and reproductive competence contribute to the reproductive phenotype. In cucurbits, for example, ethylene-related pathways and other hormonal mechanisms play major roles in determining floral sex expression (Li *et al.* 2012; Boualem *et al.* 2015). At the same time, genotype × environment interactions determine how these regulatory networks respond to changing field conditions. Advances in quantitative genetics, genome-wide association studies, genomic selection, transcriptomics and genome editing increasingly provide opportunities to identify and manipulate complex regulatory networks. Genomic selection is particularly promising for complex quantitative traits because it can exploit genome-wide marker information to predict breeding values, while its application is increasingly being investigated in fruit and vegetable crops (Lee *et al.* 2024; Xu *et al.* 2020). Genome-editing technologies, particularly CRISPR/Cas systems, have likewise expanded the possibilities for precise manipulation of genes controlling important agronomic and reproductive traits in vegetable crops (Kim *et al.* 2021; Das *et al.* 2023).

In parallel, high-throughput imaging and artificial-intelligence-assisted phenotyping offer opportunities to quantify flowering dynamics and reproductive traits at a resolution that was previously difficult to achieve. Plant phenomics increasingly integrates imaging, computer vision, machine learning and deep learning to enable automated and non-invasive measurement of complex plant traits (Singh *et al.* 2016). Such approaches could facilitate the extraction of temporally resolved traits such as flowering onset, flowering intensity, flowering duration and potentially the synchrony between male and female reproductive events across large breeding populations.

Therefore, breeding for flowering synchrony represents a shift from selecting simply for when plants flower toward selecting for how effectively their reproductive processes are coordinated. Such an approach may be particularly valuable for vegetable crops where fruit or seed production depends on precise temporal relationships among flowers, reproductive organs, parental genotypes and pollinators. It may also contribute to the development of cultivars capable of maintaining reproductive coordination under increasingly variable environmental conditions.

In this review, we synthesize the physiological, genetic, environmental and molecular determinants of flowering synchrony in vegetable crops, with particular emphasis on the coordination of flowering, sex expression, anthesis, pollen availability and stigma receptivity. We examine the diversity of reproductive synchrony across major vegetable crop groups and discuss how conventional breeding, quantitative genetics, genomic selection, genome editing and multi-omics can be integrated to manipulate this trait. We further consider advances in precision phenotyping and the challenges imposed by climate variability and propose a framework for developing climate-resilient vegetable cultivars with stable reproductive synchrony and improved reproductive efficiency.

Flowering synchrony: concepts, scales and phenotypic components

Flowering synchrony describes the temporal coordination of reproductive developmental events that determine the opportunity for successful pollination and fertilization. Although flowering time is commonly quantified as the number of days from sowing or emergence to first flowering or a defined flowering threshold, synchrony represents a broader temporal property. It considers not only when flowering begins, but also the distribution and overlap of flowering events among flowers, plants or reproductive individuals, as well as the coordination between male and female reproductive functions (Shelton *et al.* 2024; Rodríguez-Pérez and Traveset 2016). Consequently, two genotypes with similar mean flowering dates may differ considerably in synchrony if their flowering is concentrated within a short period in one genotype but dispersed over a prolonged period in another. This distinction is particularly relevant to reproductive success because flowering schedules can influence mating opportunities, pollinator interactions and subsequent fruit or seed production (Shelton *et al.* 2024; Rodríguez-Pérez and Traveset 2016).

Conceptual dimensions of flowering synchrony

Flowering synchrony can be considered at several temporal and biological levels. At the simplest level, flowering onset synchrony refers to the similarity in the timing of flowering initiation among plants. However, reproductive coordination extends beyond the onset of flowering to include the duration, intensity and progression of flowering. A genotype with a narrow and concentrated flowering period may provide greater temporal overlap among flowers than a genotype with the same flowering onset but an extended and irregular flowering period. Therefore, flowering synchrony should ideally be considered as a combination of timing, duration and overlap rather than as a single calendar date (Shelton *et al.* 2024; Ims 1990).

At the reproductive-organ level, synchrony involves the temporal relationship between pollen release and stigma receptivity. Anthesis does not necessarily coincide with maximum pollen viability or peak stigma receptivity and these processes can respond differently to developmental and environmental cues (Zinn *et al.* 2010; Hedhly 2011). The period during which viable pollen is available and the stigma is receptive can therefore be regarded as an effective reproductive window. A greater overlap between these two windows increases the potential for successful pollination, whereas temporal separation can lead to pollen–stigma mismatch even when flowering itself appears normal (Zinn *et al.* 2010; Hedhly 2011).

Synchrony may also occur between different plants or parental populations. This is particularly important in cross-pollinated and hybrid seed crops, where flowering of the male and female parents must overlap sufficiently for pollen transfer. Thus, synchrony has both an intra-genotypic component, describing coordination among flowers within an individual or population and an inter-genotypic component, describing coordination between genetically distinct populations or parental lines (Rodríguez-Pérez and Traveset 2016; Padmini *et al.* 2007).

Scales of flowering synchrony

The concept of synchrony can be organized into a hierarchical framework extending from individual flowers to crop populations. Intra-plant synchrony refers to the temporal coordination of flowering events among flowers on the same plant. It is influenced by plant architecture, inflorescence structure, branching pattern and the developmental sequence of individual flowers. In crops with prolonged flowering, successive flowers may develop asynchronously, resulting in a broad distribution of anthesis dates. The degree of intra-plant synchrony can influence the concentration of pollination events and subsequent fruit development (Shelton *et al.* 2024; Rodríguez-Pérez and Traveset 2016).

Inter-plant synchrony describes the degree to which individual plants within a cultivar or population flower during the same period. High inter-plant synchrony can produce a concentrated flowering flush, whereas asynchronous populations may exhibit extended flowering. This distinction has implications for pollination efficiency and interactions with pollinators by altering the temporal availability and abundance of floral resources (Shelton *et al.* 2024; Rodríguez-Pérez and Traveset 2016). Recent work has demonstrated that variation in individual flowering schedules and the number of flowering days can strongly influence flowering synchrony and mating opportunities within populations (Shelton *et al.* 2024).

In crops possessing separate male and female flowers or plants, reproductive success depends on synchronization between male and female flowering. This is particularly important in cucurbits and dioecious crops. In monoecious crops, for example, the timing of male and female flower production can determine whether viable pollen is available when female flowers reach anthesis. Genetic and environmental factors that alter sex expression can consequently affect the temporal availability of male and female reproductive structures (Boualem *et al.* 2015). Pollen–stigma synchrony represents a more precise reproductive level in which the period of viable pollen availability overlaps with the period of stigma receptivity. This is arguably a more functionally relevant level of synchrony because flowering overlap alone does not guarantee fertilization. Pollen viability, anther dehiscence, stigma receptivity, pollen germination and pollen-tube growth collectively determine the effective fertilization window (Hedhly 2011).

Environmental stress during flowering can alter these reproductive components and thereby reduce the probability of successful fertilization. Temperature stress, in particular, can affect pollen development, pollen viability, pollen germination and other components of plant sexual reproduction (Hedhly 2011). Thus, plants or genotypes with apparently similar flowering times may nevertheless differ in reproductive success when reproductive organs respond differently to environmental conditions.

At the population scale, synchrony determines the temporal concentration of reproductive activity across a crop. In hybrid seed production, the concept becomes particularly important because the flowering periods of male and female parental lines must overlap adequately. Differences in flowering time, flowering duration or pollen shedding can therefore result in inefficient pollen transfer and reduced hybrid seed production. Experimental work in onion, for example, has demonstrated that insufficient flowering synchrony between cytoplasmic male-sterile and pollinator parental lines can limit pollen availability and hybrid seed production, while adjustment of planting time can improve parental flowering synchronization (Padmini *et al.* 2007).

Phenotypic components of flowering synchrony

Synchrony is a multidimensional trait so; it cannot be adequately described using a single phenological measurement. Several complementary traits can be used to characterize the reproductive timeline and they are given in table 1.

Table 1 – Traits used to characterize the reproductive timeline

Component	Possible measurement	Relevance to synchrony
Days to first flowering	Days from emergence/transplanting to first flower	Determines flowering onset
Days to 50% flowering	Time required for 50% of plants/flowers to flower	Population-level flowering timing
Flowering duration	Period between first and final flowering	Determines length of reproductive window
Flowering intensity	Number of flowers produced per unit time	Describes concentration of flowering
Anthesis time	Time of individual flower opening	Determines pollination opportunity
Pollen shedding period	Duration of viable pollen release	Defines male reproductive window
Pollen viability	Percentage of viable pollen over time	Determines functional pollen availability
Stigma receptivity	Duration/intensity of stigma receptivity	Defines female reproductive window
Male–female overlap	Temporal overlap between male and female flowers	Important in monoecious/dioecious crops
Pollen–stigma overlap	Intersection of pollen availability and stigma receptivity	Direct measure of reproductive synchrony
Fruit/seed set	Proportion of flowers resulting in reproductive success	Functional consequence of synchrony

This framework also highlights why conventional descriptors such as days to flowering may be insufficient. For example, genotype A may begin flowering at 40 days and produce most flowers between 40 and 50 days, whereas genotype B may also begin flowering at 40 days but continue producing flowers until 70 days. Their flowering onset is identical, yet their degree of flowering concentration and synchrony is markedly different. Flowering

phenology can therefore be characterized using multiple quantitative dimensions, including flowering onset, flowering duration, distribution of flowering events and synchrony among individuals, rather than relying on a single flowering-time measurement (Nagahama and Yahara 2019; Freitas and Bolmgren 2008). Studies of flowering synchrony have similarly demonstrated that measures based solely on onset or variance may fail to capture the extent of temporal overlap among individuals (Freitas and Bolmgren 2008; van der Meer and Jacquemyn 2015).

From flowering time to a quantitative synchrony phenotype

For breeding purposes, flowering synchrony needs to be converted from a qualitative observation into a measurable phenotype. One simple approach is to quantify the overlap between reproductive windows:

$$\text{Synchrony Index} = \frac{\text{Duration of overlapping reproductive period}}{\text{Total reproductive period}}$$

For example, the overlap between pollen availability and stigma receptivity could be used to generate a pollen–stigma synchrony index. Similarly, the overlap between male and female flowering periods could provide a male–female synchrony index(Freitas and Bolmgren 2008).

However, a useful breeding-oriented synchrony metric should ideally incorporate more than simple temporal overlap. The biological importance of each day within the overlap period may differ according to pollen viability, stigma receptivity and flower abundance. Therefore, a more comprehensive conceptual framework could weight temporal overlap according to reproductive activity (van der Meer and Jacquemyn 2015; Arroyo-Correa *et al.* 2024):

$$RS = \sum_{t=1}^{T} P(t) \times S(t) \times F(t)$$

Where P(t) represents viable pollen availability, S(t) represents stigma receptivity and F(t) represents flowering intensity at time t. Such an approach would distinguish between a short period of intense reproductive compatibility and a longer period characterized by very low pollen or flower availability (Wadgymar *et al.* 2015; Neupane *et al.* 2023). This provides an opportunity to move toward a quantitative reproductive synchrony phenotype that can be incorporated into QTL mapping, GWAS, genomic selection and multi-environment breeding trials (Su *et al.* 2024).

Synchrony versus uniformity

Flowering synchrony should also be distinguished from flowering uniformity. Uniformity generally describes the similarity of developmental stages among individuals, whereas synchrony specifically concerns temporal overlap of reproductive events. A population can exhibit relatively uniform flowering onset but still have poor pollen–stigma synchrony if pollen maturation or stigma receptivity differs among flowers. Conversely, variation in flowering onset does not necessarily eliminate reproductive synchrony if the flowering periods are sufficiently broad to overlap. Quantitative studies have consequently emphasized that synchrony cannot always be adequately represented by a single measure of flowering onset, because individuals with different flowering schedules can still exhibit substantial temporal overlap (Freitas and Bolmgren 2008; van der Meer and Jacquemyn 2015; Arroyo-Correa *et al.* 2024; Wadgymar *et al.* 2015).

This distinction is particularly important under environmental stress. A genotype may display stable mean flowering time across environments but show large changes in flowering duration or reproductive overlap. Multi-environment studies of flowering traits demonstrate that environmental conditions can modify the expression and genetic architecture of phenology-related traits, including genotype × environment interactions (Neupane *et al.* 2023; Su *et al.* 2024). Consequently, breeding for synchrony should consider not only the mean phenotype but also the stability of reproductive overlap across environments.

Physiological determinants of reproductive coordination

Reproductive coordination is governed by a sequence of physiological processes that connect the transition to flowering with successful pollination and fertilization. The timing of floral induction, floral initiation and subsequent flower development establishes the basic reproductive calendar of a plant, while developmental rates determine whether individual flowers and inflorescences progress through reproductive stages simultaneously. The transition from vegetative to reproductive growth is influenced by endogenous developmental status as well as carbohydrate availability, hormonal balance and environmental signals (Moghaddam and Ende 2013; Amasino and Michaels 2010; Sonnewald and Fernie 2018; Conti 2017). Once floral meristems are established, differences in the rate of floral organ development can generate variation in anthesis among flowers within the same plant or among plants of the same genotype. Thus, synchrony is ultimately a consequence not only of the timing of floral initiation but also of the coordinated progression of reproductive development toward anthesis (Amasino and Michaels 2010; Sonnewald and Fernie 2018).

The rate and timing of anthesis constitute another important physiological component of reproductive coordination. Flower opening is frequently regulated by diurnal rhythms and is influenced by temperature, light and endogenous circadian processes (van Doorn and Van Meeteren 2003; Shi *et al.* 2026). The timing of anthesis determines when anthers and stigmas become exposed to pollinators and when pollen becomes available for transfer. However, anthesis does not necessarily coincide with maximum reproductive competence. Anthers may require additional time for pollen maturation and dehiscence, while stigma receptivity may begin before or after flower opening and may persist for a different duration (Zinn *et al.* 2010; Hedhly 2011). Consequently, variation in the timing of flower opening, anther dehiscence and stigma maturation can alter the effective period during which pollination can occur.

Pollen performance and pistil receptivity therefore represent critical physiological determinants of reproductive synchrony. Pollen viability is determined by the completion of microsporogenesis, pollen maturation, dehydration and subsequent physiological activation during germination. Following pollen deposition, successful reproduction additionally requires a receptive stigma, pollen hydration and germination, pollen-tube growth and fertilization *(Zinn et al.* 2010; Hedhly 2011; Dresselhaus *et al.* 2016). The duration of pollen viability and stigma receptivity can differ substantially among crops and genotypes, creating reproductive windows of different widths. Synchrony is therefore expected to be greatest when viable pollen availability overlaps with the period of stigma receptivity. Conversely, premature pollen release, delayed anther dehiscence or shortened stigma receptivity can produce pollen–stigma mismatch even when male and female flowers appear synchronized at the level of anthesis (Zinn *et al.* 2010; Hedhly 2011; Dresselhaus *et al.* 2016).

Plant source–sink relationships and hormonal regulation further influence reproductive coordination. Developing flowers and reproductive organs represent strong sinks for assimilates and carbohydrate availability can affect floral development, flower retention and subsequent fruit or seed set (Sonnewald and Fernie 2018; Yu *et al.* 2015). Sugars also function as signalling molecules that integrate plant developmental status with reproductive transitions and interact with hormonal and circadian pathways (Moghaddam and Ende 2013). Hormones including gibberellins, auxins, cytokinins, ethylene and abscisic acid participate in the regulation of flowering, floral organ development and reproductive processes, although their relative effects vary among species and developmental contexts (Conti 2017; Boualem *et al.* 2015). This is particularly evident in cucurbits, where hormonal regulation contributes to the determination of floral sex. Ethylene biosynthesis and signalling have a central role in cucurbit sex expression, while gibberellin-mediated pathways can also influence floral sex development (Boualem *et al.* 2015; Nguyen *et al.* 2024). Changes in assimilate availability or hormonal balance can therefore modify reproductive development and, in some crops, the timing and distribution of flowers, potentially affecting synchrony.

The physiological coordination of reproduction is highly responsive to the surrounding environment, making synchrony a dynamic rather than fixed trait. Temperature can alter developmental rates, anthesis, pollen maturation and reproductive organ function, while water and nutrient availability can modify assimilate partitioning and reproductive development (Zinn *et al.* 2010; Hedhly 2011). Importantly, these processes may respond at different rates or thresholds to the same environmental stimulus, creating temporal mismatches between otherwise coordinated reproductive events. Temperature stress, for example, can impair pollen development, pollen viability, pollen germination and other components of plant sexual reproduction (Zinn *et al.* 2010; Hedhly 2011). Consequently, an important physiological component of breeding for flowering synchrony is not simply achieving a particular flowering date, but maintaining stable coordination among floral development, anthesis, pollen availability and pistil receptivity across variable environmental conditions.

This physiological perspective provides the basis for examining the genetic mechanisms that regulate flowering and reproductive coordination in vegetable crops.

Genetic architecture of flowering and sex expression and environmental regulation

Flowering time and sex expression in vegetable crops are complex quantitative traits controlled by multiple genes and strongly modified by environmental conditions. Genetic variation in the timing of the vegetative-to-reproductive transition, floral meristem development, flowering duration and flower number provides the basis for breeding cultivars with distinct reproductive calendars. Conserved flowering pathways involving photoperiod perception, circadian-clock components, florigen production and floral meristem identity contribute to this variation (Song *et al.* 2015; Andrés and Coupland 2012; Srikanth and Schmid 2011), while crop-specific genetic networks modify the magnitude and direction of these effects. Quantitative trait loci (QTLs), genome-wide association studies (GWAS) and transcriptomic analyses have identified genomic regions associated with flowering time and related reproductive traits in several vegetable crops. For example, QTL mapping and QTL-seq in cucumber have identified loci controlling flowering time, including a major early-flowering QTL associated with the FT-related flowering pathway (Lu *et al.* 2014; Wang *et al.* 2020a). GWAS of cucumber germplasm has additionally identified genomic regions associated with flowering-time variation (Wang *et al.* 2018). However, because flowering synchrony represents the coordination of several developmental processes, its genetic architecture is likely to involve both major flowering regulators and loci controlling the rate and stability of downstream reproductive development.

The genetic regulation of sex expression adds another layer of complexity, particularly in cucurbit vegetables and other crops exhibiting monoecious, dioecious or sex-variable reproductive systems. The proportion and

distribution of male, female and hermaphroditic flowers can strongly influence opportunities for cross-pollination and fruit production. In cucurbits, genetic determinants of sex expression interact with hormonal pathways, particularly ethylene-mediated signalling, to regulate the developmental fate of floral primordia (Boualem *et al.* 2015; Li *et al.* 2019; Yamasaki *et al.* 2005). Consequently, genetic differences affecting sex determination can alter not only the number of flowers of a particular sex but also their distribution along the plant. From a breeding perspective, synchronizing male and female flower production therefore requires consideration of both flowering-time genes and genetic factors governing sex expression, making reproductive synchrony a trait that emerges from the interaction of multiple genetic pathways.

Environmental factors further modify the expression of these genetic programs, with temperature and photoperiod being among the most important determinants of flowering phenology. Temperature influences developmental rates and flowering behaviour, whereas photoperiod regulates the timing of floral transition through interactions between light perception and the circadian clock (Song *et al.* 2015; Andrés and Coupland 2012; Srikanth and Schmid 2011). Water availability, nutrient status, light intensity and spectral quality can additionally modify flowering and reproductive development by altering plant growth, assimilate availability and hormonal balance (Sonnewald and Fernie 2018; Zinn *et al.* 2010). In cucurbits, environmental conditions can substantially modify the ratio and distribution of male and female flowers, while temperature and photoperiod can shift flowering and sex-expression behaviour in cucumber and related crops (Nguyen *et al.* 2024; Li *et al.* 2019). Thus, environmental conditions can influence different components of reproductive synchrony independently, potentially producing a mismatch between flowering, pollen availability and stigma receptivity.

These interactions make genotype × environment (G×E) effects particularly important when breeding for stable flowering synchrony. A genotype selected for early or synchronized flowering under one environment may display substantially different flowering duration, sex expression or reproductive overlap when exposed to another temperature regime, photoperiod or water-availability condition. QTL studies have demonstrated that the magnitude of flowering-related genetic effects can vary across environments, providing evidence that flowering phenology is subject to G×E interactions (Malmberg and Mauricio 2005; El-Soda *et al.* 2014). Multi-environment trials, reaction-norm analysis and genomic approaches can therefore help identify alleles associated with both flowering performance and environmental stability (Malmberg and Mauricio 2005; Xiong *et al.* 2026). Ultimately, the most useful breeding material may not be the genotype with the earliest or most concentrated flowering, but one that maintains an appropriate overlap among flowering, male and female reproductive functions and pollination windows despite environmental fluctuations.

Molecular networks governing flowering synchrony

Flowering synchrony is the outcome of interconnected molecular pathways that integrate endogenous developmental status with environmental signals to regulate the timing and progression of reproductive development. Rather than being controlled by a single flowering pathway, reproductive coordination emerges from interactions among the photoperiodic, circadian-clock, temperature, hormonal, carbohydrate and floral-development networks (Song *et al.* 2015; Andrés and Coupland 2012). Environmental information is perceived through photoreceptors and temperature-sensing mechanisms and subsequently integrated with the circadian clock, allowing plants to adjust flowering to seasonal and daily conditions. These signals converge on key flowering regulators, including CONSTANS (CO), FLOWERING LOCUS T (FT), SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1 (SOC1), LEAFY (LFY) and APETALA1 (AP1), which progressively establish flowering competence and floral identity (Song *et al.* 2015; Conti 2017; Amasino and Michaels 2010). Variation in the activity or environmental sensitivity of these regulatory nodes can consequently alter flowering time and flowering pattern and may contribute to differences in reproductive synchrony (Rodríguez-Pérez and Traveset 2016).

The photoperiodic and circadian-clock networks provide an important molecular basis for temporal coordination. Photoreceptors such as phytochromes and cryptochromes perceive changes in light quantity and quality, while circadian components generate endogenous rhythms that regulate the timing of downstream flowering signals (Amasino and Michaels 2010; Shi *et al.* 2026). The interaction of clock-associated proteins with GIGANTEA (GI), FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1) and CO contributes to the photoperiodic regulation of FT expression in leaves (Shi *et al.* 2026; Song *et al.* 2015). FT or FT-like proteins subsequently act as mobile florigenic signals that promote flowering at the shoot apical meristem, where they interact with meristem-identity regulators and activate genes such as SOC1, LFY and AP1 (Song *et al.* 2015). Because these pathways integrate information over time rather than responding simply to a single environmental stimulus, changes in circadian phase, photoperiod sensitivity or FT activation can alter the timing of flowering and potentially influence temporal coordination among plants and reproductive structures.

Temperature-responsive pathways interact closely with photoperiodic and circadian regulation to adjust flowering under changing thermal conditions. Temperature can modify the expression and activity of flowering regulators as well as chromatin states associated with flowering competence (Capovilla et al. 2015; Quint *et al.* 2016). In model systems, thermosensory mechanisms involving PHYTOCHROME INTERACTING FACTORS (PIFs), chromatin-associated processes and temperature-responsive changes in flowering repressors contribute to seasonal adjustment of flowering (Capovilla *et al.* 2015; Quint *et al.* 2016). These mechanisms are particularly relevant to reproductive synchrony because temperature can simultaneously influence floral transition and the

subsequent development of reproductive organs. Thus, temperature-dependent changes in flowering signals may occur alongside independent effects on pollen maturation, anther dehiscence and stigma receptivity, creating potential reproductive mismatches under fluctuating environments (Hedhly 2011).

Hormonal and metabolic pathways provide additional layers of molecular integration. Gibberellins, auxins, cytokinins, ethylene and abscisic acid interact with flowering regulators and contribute to floral initiation, floral organ development and reproductive processes (Srikanth and Schmid 2011). Ethylene signalling is particularly important for regulating female flower development in several cucurbits, whereas gibberellin-related pathways can promote or modify male flower development depending on species and developmental context (Boualem *et al.* 2015; Yamasaki *et al.* 2005). Carbohydrate signalling also links photosynthetic status with reproductive development through molecules such as sucrose and trehalose-6-phosphate, allowing flowering responses to be integrated with plant carbon status (Moghaddam and Ende 2013). The convergence of these hormonal and metabolic signals with the core flowering network means that changes in resource availability can influence the timing and developmental competence of reproductive structures.

At the downstream level, molecular regulation extends from floral induction to pollen development, anther maturation, stigma receptivity and pollen–pistil interactions. Transcription factors, hormone signalling networks, reactive oxygen species, calcium signalling and tissue-specific gene expression contribute to the maturation and functional competence of reproductive organs (Dresselhaus *et al.* 2016; Zinn *et al.* 2010). Importantly, these processes do not necessarily respond synchronously to environmental or developmental signals. Consequently, a genotype may maintain relatively normal floral induction while exhibiting altered pollen viability or reproductive function under stress (Zinn *et al.* 2010; Hedhly 2011). This highlights the need to view flowering synchrony as an emergent property of interconnected molecular networks, rather than as a direct consequence of individual flowering-time genes. Integrating knowledge of these networks with genomic selection, transcriptomics and genome editing could therefore provide opportunities to manipulate regulatory nodes associated with flowering and reproductive stability in vegetable crops.

Pollination biology and pollen–stigma synchrony

Pollination represents the critical biological link between flowering and successful sexual reproduction and its efficiency depends strongly on the temporal coordination between pollen availability and stigma receptivity. Flower opening alone does not necessarily indicate that a flower is fully competent for fertilization, because pollen maturation, anther dehiscence and stigma receptivity may occur at different developmental times (Dresselhaus *et al.* 2016). The period during which viable pollen is available must therefore overlap with the period during which the stigma can effectively capture, hydrate and support pollen germination. This pollen–stigma synchrony can be considered a functional component of reproductive synchrony and defines an important part of the effective reproductive window within which successful pollination can occur. The duration and timing of this window vary among species and are influenced by genotype, floral morphology, reproductive system and environmental conditions (Dresselhaus *et al.* 2016; Zinn *et al.* 2010).

Pollen performance is determined by several sequential processes, including microspore development, pollen maturation, anther dehiscence, pollen release, pollen viability and subsequent germination on the stigma. Following deposition, compatible pollen must hydrate and germinate on the stigma before the pollen tube penetrates the style and reaches the ovule (Zinn *et al.* 2010; Dresselhaus *et al.* 2016; Johnson *et al.* 2019). In parallel, the stigma undergoes developmental and biochemical changes that determine its receptivity, including changes in surface characteristics, secretions, hydration status and molecular recognition mechanisms (Johnson *et al.* 2019). Consequently, reproductive success depends not only on whether pollen and stigma are present simultaneously but also on whether both are physiologically competent at the time of interaction. This distinction is particularly important when evaluating synchrony in breeding populations, because apparent overlap in anthesis may not translate directly into effective fertilization.

The importance of pollen–stigma synchrony varies with the reproductive system of the crop. In self-compatible vegetables, synchrony between anther dehiscence and stigma receptivity can influence the probability and efficiency of self-pollination, whereas cross-pollinated crops require adequate temporal overlap between compatible pollen sources and receptive stigmas. In self-incompatible crops such as many Brassica vegetables, reproductive success additionally depends on the recognition of compatible pollen, meaning that both temporal and genetic compatibility must coincide (Takayama and Isogai 2005). In monoecious cucurbits, the timing and abundance of male and female flowers introduce another layer of coordination, because female flowers require viable pollen during their receptive period (Boualem *et al.* 2015; Yamasaki *et al.* 2005). In hybrid seed production, synchronization becomes even more important because flowering and pollen shedding of the male parent must overlap with receptive flowers of the female parent (Colombo and Galmarini 2017).

Pollination synchrony is also strongly influenced by environmental conditions and interactions with pollinators. Temperature, humidity, rainfall and light can modify anthesis, anther dehiscence, pollen viability and stigma receptivity, while environmental stress may affect male and female reproductive functions at different rates (Zinn *et al.* 2010). In insect-pollinated vegetables, the temporal activity of pollinators introduces an additional biological component: flowers must not only be receptive when pollen is available but also be accessible when effective pollinators are active. Floral traits such as flower opening time, nectar production, colour and volatile emissions can influence pollinator visitation and may themselves show environmental and circadian regulation (van Doorn

and Van Meeteren 2003; Kessler and Baldwin 2007). Thus, reproductive synchrony can be viewed as a multi-level temporal interaction involving flower development, pollen availability, stigma receptivity and pollinator activity.

From a breeding perspective, pollen–stigma synchrony provides a potentially more functionally meaningful measure of reproductive coordination than flowering date alone. Traits such as pollen viability over time, anther dehiscence, stigma receptivity, anthesis time and the duration of their overlap could be incorporated into phenotyping and genetic analyses. Quantifying this overlap across contrasting environments could help identify genotypes with stable reproductive windows and improved fruit or seed set. Such approaches are particularly relevant under climate change, where temperature extremes can shift flowering and reproductive processes at different rates, increasing the risk of pollen–stigma mismatch (Zinn *et al.* 2010; Hedhly 2011). Therefore, future breeding programs could consider pollen–stigma synchrony as an integrated reproductive trait linking flowering phenology to reproductive success, rather than treating pollen and pistil traits entirely as independent components.

Flowering synchrony across major vegetable crops

The biological significance of flowering synchrony differs substantially among vegetable crops because reproductive systems, floral architecture, pollination mechanisms and the importance of fruit versus seed production vary among crop groups. Consequently, synchrony cannot be defined using a single phenotypic criterion across vegetables. In some crops, synchronization primarily concerns the concentration of flowering and anthesis, whereas in others it involves coordination between male and female flowers, compatible parental lines, or pollen availability and stigma receptivity. A comparative understanding across vegetable groups is therefore important for identifying crop-specific breeding targets and avoiding the assumption that mechanisms governing flowering synchrony in one reproductive system can be directly applied to another(Kessler and Baldwin 2007).

Solanaceous vegetables

Tomato, pepper and eggplant predominantly possess bisexual flowers, making synchrony primarily relevant to the coordination of floral development, anthesis, pollen maturation, stigma receptivity and subsequent fruit set. In tomato, flowering occurs progressively along the inflorescence and differences in flowering rate and flower retention influence the temporal distribution of fruit development and harvest. Synchronization of flowering with pollen viability and suitable environmental conditions is particularly important because high temperatures can impair pollen development, pollen viability, pollen germination, female reproductive function and fruit set (Driedonks *et al.* 2016; Camejo *et al.* 2005). In pepper and eggplant, flowering and fruit set are likewise influenced by temperature and plant developmental status. For these crops, breeding for synchrony therefore involves maintaining a predictable flowering pattern while preserving pollen fertility, stigma function and fruit-set capacity under variable environments. In hybrid seed production, synchronization between parental lines is an additional consideration, particularly where differences in flowering duration or anthesis timing can limit effective crossing (Colombo and Galmarini 2017).

Cucurbit vegetables

Cucurbits provide one of the clearest examples of the interaction between flowering synchrony and reproductive biology because many species exhibit monoecious, gynoecious or other sex-expression systems. Cucumber, melon, watermelon, pumpkin and squash can differ considerably in the timing and distribution of male and female flowers. Consequently, reproductive success depends not only on the overall onset of flowering but also on the temporal overlap between male pollen production and female flower receptivity. Sex expression is strongly influenced by genetic background, developmental stage, hormones and environmental conditions, particularly temperature and photoperiod (Zinn *et al.* 2010; Hedhly 2011; Dhall *et al.* 2023a). In cucumber, for example, genetic variation for gynoecy and flowering behaviour is widely exploited in hybrid breeding, while manipulation of male and female flowering can facilitate hybrid seed production (Dhall *et al.* 2023a; Tao *et al.)*. Synchrony in cucurbits is therefore a multidimensional trait involving flowering time, flower sex, node position, flower abundance, anthesis, pollen availability and stigma receptivity. This makes cucurbits particularly valuable models for studying reproductive synchrony as a breeding target.

Brassicaceous vegetables

Cabbage, cauliflower, broccoli, radish, turnip and related Brassica vegetables exhibit a different form of reproductive coordination because flowering is strongly influenced by developmental age and environmental cues such as temperature and photoperiod. Many Brassica vegetables have strong vernalization requirements, making the transition from vegetative growth to reproductive development a major determinant of flowering time and uniformity (Amasino and Michaels 2010; Song *et al.* 2015). Variation in vernalization response can lead to substantial differences in bolting and flowering among genotypes. Once flowering occurs, reproductive synchrony is further influenced by inflorescence development, anthesis, pollen release and stigma receptivity. In self-incompatible Brassica crops, the timing of flowering must additionally coincide with the availability of genetically compatible pollen. These characteristics make synchronization particularly important in hybrid seed production, where male and female parental lines must flower and release viable pollen during overlapping periods (Takayama

and Isogai 2005; Colombo and Galmarini 2017). Breeding for appropriate vernalization response, flowering stability and parental synchronization can therefore improve seed-production efficiency.

Leguminous vegetables

Pea, common bean, cowpea and other leguminous vegetables display considerable variation in flowering time, flowering duration and environmental sensitivity. Photoperiod, temperature and plant developmental status influence the transition to flowering, while assimilate availability and reproductive resource allocation affect flower retention and pod development (Summerfield *et al.* 1996; Craufurd and Wheeler 2009). In some legumes, asynchronous flowering can extend the reproductive period and contribute to uneven pod maturity, whereas greater concentration of flowering can improve harvest uniformity in production systems where synchronized maturity is desirable. At the reproductive level, pollen viability, stigma receptivity and floral morphology interact with pollination mechanisms to determine reproductive success. Consequently, breeding objectives may differ according to production purpose: synchronization can be desirable for concentrated vegetable harvest, whereas a somewhat extended flowering period may contribute to yield stability under environmental stress.

Dioecious and other specialized vegetable crops

Dioecious vegetables such as spinach and asparagus present a distinct synchronization challenge because male and female reproductive functions occur on separate plants. Successful seed production therefore requires sufficient temporal overlap between male pollen release and female flower receptivity. Similar considerations apply to crops in which male sterility, self-incompatibility or other reproductive barriers are exploited for hybrid seed production. In these systems, synchronization is not simply a property of an individual genotype but an interaction between parental flowering calendars and reproductive compatibility. Differences in flowering time or duration between parental populations can reduce crossing efficiency and seed yield. Selection for compatible flowering windows, together with environmental manipulation and staggered planting, can therefore become an important component of seed-production breeding strategies (Colombo and Galmarini 2017; Padmini *et al.* 2007).

Conventional and molecular breeding for flowering synchrony

Breeding for flowering synchrony has traditionally been approached indirectly through selection for flowering time, flowering duration, sex expression, male and female fertility and parental compatibility. In vegetable crops, this is particularly evident in hybrid seed production, where successful crossing requires appropriate overlap between flowering periods of parental lines (Colombo and Galmarini 2017). Conventional breeding therefore begins with the identification of genetic variation for flowering behaviour followed by selection for desirable flowering windows under target production environments. In tomato, quantitative genetic analysis has demonstrated that flowering time is genetically dissectable into several developmental components rather than representing a single trait. A QTL study using a *Solanum lycopersicum* × *S. pimpinellifolium* population identified QTLs for days to flowering, leaf number, floral induction, flower-bud appearance and flower-development duration, with major QTLs on chromosomes 1 and 6 explaining a substantial proportion of flowering-time variation. Interestingly, several developmental traits co-localized with flowering-time QTLs, suggesting that selection for flowering time can indirectly modify the rate of reproductive development (Sumugat *et al.* 2010). Such results provide a foundation for synchrony breeding, but also demonstrate why selecting solely for days to flowering may be insufficient: breeders may need to select simultaneously for flowering onset, developmental rate and flowering duration to obtain a concentrated and reproducible reproductive window.

In cucurbits, conventional breeding has made particularly effective use of sex-expression variation to improve reproductive coordination and hybrid seed production. Cucumber provides a strong example, where gynoecious lines produce predominantly or exclusively female flowers and have been extensively exploited as female parents in hybrid breeding. The genetic basis of sex expression involves major loci and modifiers, including the F, M and A loci, which are associated with members of the aminocyclopropane-1-carboxylic acid synthase (ACS) family and consequently with ethylene biosynthesis. Molecular-marker-based selection for these loci allows breeders to identify desirable sex phenotypes before extensive field evaluation (Wang *et al.* 2020b; Dhall *et al.* 2023b). This has a direct connection to flowering synchrony: rather than attempting to synchronize large numbers of individual male and female flowers manually, breeders can modify the composition and temporal distribution of floral sexes so that female flowers are produced during periods when pollen from the male parent is available. Gynoecious cucumber therefore represents an important example in which manipulation of a reproductive trait indirectly improves synchrony and makes hybrid seed production more efficient. Similar exploitation of gynoecy has been reported in other cucurbits, including bitter gourd and melon (Singh *et al.* 2023).

A second conventional strategy is the use of male sterility and self-incompatibility to control the direction and efficiency of pollination. Genic male sterility, cytoplasmic–genic male sterility and self-incompatibility systems have been exploited across vegetable crops, particularly Brassicaceae and Solanaceae, to eliminate or restrict self-pollination and facilitate hybrid seed production. Such systems do not themselves synchronize flowering, but they increase the importance of parental flowering overlap because the female parent depends on pollen from the designated male parent. Consequently, selection for male-sterile or self-incompatible female lines should ideally be combined with evaluation of flowering date, anthesis, pollen shedding and stigma receptivity of the corresponding male parent. Reviews of vegetable hybrid breeding emphasize that knowledge of anthesis time,

anther dehiscence and pollen fertility is essential for efficient hybrid seed production and that unsynchronized flowering can substantially complicate crossing operations (Colombo and Galmarini 2017). This provides a practical breeding route for synchrony: combine reproductive-control systems with complementary flowering phenology, rather than treating flowering time and pollination control as independent breeding objectives.

Molecular breeding provides an opportunity to move from phenotypic selection toward more precise manipulation of flowering and reproductive coordination. The cucumber sex-determination system provides one of the clearest vegetable examples. Beyond marker-assisted selection, functional studies have demonstrated that modification of CsWIP1 can generate gynoecious cucumber plants, while ACS-family genes regulate ethylene-mediated sex determination (Sumugat *et al.* 2010). This principle could be extended from sex expression to flowering synchrony by targeting genes or regulatory elements controlling flowering-time sensitivity, floral transition and environmental responsiveness. Importantly, genome editing need not be restricted to complete gene knockouts; promoter or cis-regulatory editing could potentially fine-tune the magnitude and timing of flowering responses and thereby produce alleles with more desirable flowering windows. Evidence from crops outside vegetables also supports this strategy conceptually, but translation to vegetables should prioritize orthologous flowering regulators and validate their effects under crop-specific environments rather than assuming that the phenotype of a model species will be conserved (Singh *et al.* 2016).

An additional molecular-breeding opportunity is to select for reproductive stability under environmental stress, rather than synchrony only under optimal conditions. Tomato provides an especially useful example. A QTL study using recombinant inbred and introgression populations derived from *S. lycopersicum* and *S. pimpinellifolium* evaluated reproductive traits under progressively higher temperature regimes and identified QTLs affecting flower number, fruit number, fruit set, stigma exsertion and pollen viability. Increasing temperature strongly reduced fruit set in the susceptible background, whereas several lines displayed considerably smaller reductions, demonstrating exploitable genetic variation for reproductive performance under heat stress (Gonzalo *et al.* 2020a). Although these QTLs were not identified specifically as "flowering synchrony" loci, they are highly relevant to the concept because reproductive coordination ultimately depends on maintaining functional pollen and pistils within the same reproductive window. Similar approaches could therefore be extended in vegetables by mapping flowering onset × anthesis × pollen viability × stigma receptivity × fruit set simultaneously across environments. This would allow breeders to distinguish genotypes that merely flower at the desired time from those that maintain stable reproductive synchrony under environmental fluctuations (Yamasaki *et al.* 2005).

Overall, the available evidence suggests that breeding for flowering synchrony should evolve from indirect selection for individual flowering traits toward an integrated reproductive-coordination strategy. Conventional selection can exploit variation in flowering time, flowering duration, sex expression and reproductive fertility; marker-assisted selection can accelerate the introgression of genes controlling these traits; and genome editing can potentially fine-tune flowering and sex-expression pathways. The most promising approach, however, is likely to combine these technologies with multi-environment phenotyping.

Precision Phenotyping and AI-Assisted Breeding for Climate-Resilient Flowering Synchrony

Conventional assessment of flowering synchrony relies largely on repeated visual observations of traits such as days to first flowering, days to 50% flowering, flower number and flowering duration. Although these measurements are useful, they are labor-intensive and often provide only a limited temporal description of reproductive development. High-throughput plant phenotyping (HTPP) offers an opportunity to transform flowering synchrony into a quantitative, time-resolved trait through repeated RGB, multispectral, hyperspectral and three-dimensional imaging (Jiang *et al.* 2020; Furbank and Tester 2011). Image-based phenotyping can capture developmental changes non-destructively and at substantially greater scale than manual scoring, while computer-vision approaches can extract traits such as flower number, developmental stage, canopy architecture and flowering intensity from sequential images (Jiang *et al.* 2020; Singh *et al.* 2018). For flowering-synchrony breeding, repeated imaging could therefore generate individual flowering trajectories rather than a single flowering-time measurement, allowing estimation of flowering onset, peak flowering, flowering duration and overlap among plants or parental lines.

Artificial intelligence can further convert these image streams into quantitative reproductive phenotypes. Deep-learning approaches based on object detection, image segmentation and classification are increasingly being applied to plant phenotyping (Singh *et al.* 2018; Kamilaris and Prenafeta-Boldú 2018). Applied specifically to flowering dynamics, Jiang et al. developed Deep Flower, a deep-learning pipeline that detected and counted individual cotton blooms from repeated field images and used the resulting data to construct flowering curves and derive flowering characteristics (Jiang *et al.* 2020). This provides direct evidence that AI-assisted phenotyping can move flowering assessment from discrete manual scores toward time-resolved flowering trajectories. Applied to flowering synchrony, similar pipelines could potentially identify individual flowers and classify developmental stages from bud formation through anthesis, while simultaneously tracking their position and timing. These data could then be combined with environmental measurements to construct flowering curves and calculate synchrony indices at plant, population and parental levels.

Importantly, phenotyping should extend beyond visible flowers to functionally relevant traits such as pollen viability and release. In tomato, pollen viability, pollen release and fruit set are important indicators of reproductive heat tolerance (Heidmann *et al.* 2016; Gonzalo *et al.* 2020b). Conventional pollen assessment can be

laborious; however, automated approaches including impedance flow cytometry have been demonstrated for rapid discrimination of viable and non-viable pollen in tomato, cucumber and pepper (Heidmann *et al.* 2016). Thus, combining AI-based flower phenotyping with automated pollen and reproductive measurements could provide a more complete estimate of functional reproductive synchrony.

Climate change makes such quantitative phenotyping particularly important because flowering synchrony may be disrupted when environmental stresses affect different reproductive processes at different rates. High temperature can alter flowering, pollen development, pollen viability, anther function and fruit set, potentially producing a mismatch between flowering and effective fertilization (Driedonks *et al.* 2016; Gonzalo *et al.* 2020b). Tomato provides a particularly well-characterized vegetable example: heat stress can substantially reduce pollen number and viability, impair pollen release and decrease fruit set, while genetic variation for these reproductive traits provides opportunities for breeding heat-tolerant cultivars (Driedonks *et al.* 2016; Gonzalo *et al.* 2020b). Therefore, climate-resilient synchrony should not simply mean maintaining an unchanged flowering date under warming conditions; rather, it should mean maintaining appropriate temporal overlap among flowering, pollen availability, stigma receptivity and fertilization despite environmental fluctuations.

A future breeding strategy could consequently combine precision phenotyping, environmental characterization and genomic prediction to identify genotypes with stable reproductive coordination across environments. Multi-environment trials could record flowering trajectories together with temperature, humidity, photoperiod and soil-water conditions, enabling breeders to estimate both synchrony and its environmental stability. Genomic selection could then potentially be used to predict breeding values for composite traits such as flowering-window stability, pollen–stigma overlap and fruit set under heat stress, while genome editing could fine-tune flowering or sex-expression pathways identified through QTL, GWAS and multi-omics analyses (Andrés and Coupland 2012; Crossa *et al.* 2017). This approach is particularly relevant for vegetables because climate-resilience breeding increasingly targets reproductive traits such as pollen viability and fruit set rather than vegetative survival alone (Driedonks *et al.* 2016; Gonzalo *et al.* 2020b). Ultimately, the objective should be to select cultivars that maintain a stable and sufficiently broad reproductive window under realistic combinations of heat, drought and other environmental stresses, thereby shifting flowering synchrony from a phenological descriptor to a measurable target for climate-resilient vegetable breeding.

CONCLUSION AND FUTURE PERSPECTIVES

Flowering synchrony should be recognized as an important but underexploited component of reproductive performance in vegetable crops. It extends beyond conventional flowering-time measurements to encompass the temporal coordination of floral initiation, anthesis, sex expression, pollen maturation and release, stigma receptivity, pollination and fertilization. The synthesis presented in this review highlights that synchrony is an emergent phenotype shaped by genetic architecture, physiological development and environmental conditions. Consequently, breeding for reproductive coordination requires consideration of the timing, duration and overlap of multiple reproductive processes, rather than selection for flowering time alone.

Future breeding efforts should establish flowering synchrony as a quantifiable composite trait using standardized indices that integrate flowering trajectories, pollen availability, stigma receptivity and reproductive success. Time-series imaging, AI-assisted phenotyping and environmental sensing can enable high-throughput measurement of these traits, while QTL mapping, GWAS, genomic selection and multi-omics can identify their genetic and molecular determinants. Genome editing, particularly precision modification of regulatory regions, offers further opportunities to fine-tune flowering and sex-expression pathways. Integrating these approaches across multi-environment trials will be essential for identifying genotypes that maintain reproductive coordination rather than simply exhibiting desirable flowering dates under a single environment.

Climate change further strengthens the need for this approach because heat, drought and environmental variability can disrupt flowering, pollen viability, stigma receptivity and pollinator activity at different rates, resulting in reproductive mismatch and reduced fruit or seed set. Therefore, the future breeding target should shift from simply early, late or uniform flowering toward stable reproductive synchrony under variable environments. An integrated pipeline combining germplasm diversity, precision phenotyping, synchrony indices, genomics, multi-omics, genome editing and multi-environment validation could transform flowering synchrony into an explicit breeding objective and contribute to the development of climate-resilient vegetable cultivars with stable pollination, fertilization and yield.

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