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Isabel Marques,
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Julieta Andrea Silva De Almeida,
Centro de Solos e Recursos Ambientais, Instituto Agronômico de Campinas (IAC), Brazil
Asaw Degu,
Agricultural Research Organization (ARO), Israel

*CORRESPONDENCE
José Raúl Rendón-Sáenz
✉ joser.rendon@cafedecolombia.com

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Unveiling triggers for flowering in coffee plants: a systematic review of endogenous and environmental factors

José Raúl Rendón-Sáenz[1]*, Carolina Zamorano-Montañez[2], Juan Carlos García-López[3], Nelson Ceballos-Aguirre[2], Miguel Alfonso Castiblanco-Carranza[4] and Juliana Vargas-López[2]

[1]Department of Crop Science, National Coffee Research Center - Cenicafé, Manizales, Colombia, [2]Faculty of Agricultural Sciences, University of Caldas, Manizales, Colombia, [3]Department of Agroclimatology, National Coffee Research Center- Cenicafé, Manizales, Colombia, [4]Documentation Center, National Coffee Research Center- Cenicafé, Manizales, Colombia

This systematic review (SR) focuses on the triggers of coffee flowering and synthesizes the main findings of scientific publications published over approximately 60 years, with the aim of analyzing the progress of studies on environmental and endogenous factors that promote flowering and prioritizing prospects for future research. Flowering studies in coffee species related to climate, soil or endogenous variables were included, and studies in other crops or phenological stages other than flowering were excluded. For the search, databases of private publishing clusters were consulted, including *Science Direct*, *Taylor and Francis* and *Springer Link*, and a second group of databases considered large indexers was integrated, namely, *Dimensions*, *Web of Science* and *SciELO*, with search dates until October 25, 2024. Of the 706 studies retrieved on environmental factors, 43 met the eligibility criteria, and of a total of 187 studies on endogenous factors, 23 were included. Among climate variables, water stress is essential for coffee flowering; the initiation of flowering can occur after a precipitation event greater than 10 mm. The development of flower buds occurs at average annual temperatures ranging from 17 to 23 °C, with a lower limit of 10 °C and an upper limit of 32 °C. The photoperiod with shortest days (less than 13–14 h of light) 2 or 3 months before flowering determines the induction of flowering at latitudes above 7°N. At the endogenous level, the MADS-box gene family, type II (MIKC), stands out for its function as a regulator of reproductive development, the flower organ identity and flower meristem determination, while the *FLOWERING LOCUS C (FLC)* gene is related to the regulation of flower induction time. During dry periods, ethylene production decreases in leaves and flower buds; later, when the plants are rehydrated, the ethylene levels increase. Future research should focus on investigating agroclimatic indices such as air vapor pressure deficit and plant physiological and functional traits, such as density and stomatal conductance.

KEYWORDS

***coffea*, phenology, flower development, flowering stage, abiotic stress, genes, phytohormones**

1 Introduction

The phenology of the coffee plant is classified into a sequence of six phases. The vegetative phase includes the formation of leaf buds, followed by the second phase of induction, maturation, and dormancy of the flower buds. The reproductive phase begins with the anthesis of the mature flower buds, the fourth phase is the formation and setting of the fruits; the fifth, the ripening of the fruits; and finally, the senescence of the branches (Camargo and Camargo, 2001).

The BBCH phenological scale describes the beginning of the reproductive phase, determined by the induction and initiation of the inflorescence, which occurs at the molecular level until the swelling of the leaf axil, from this the buds of the inflorescence emerge between the stipules, then flower buds adhered to each other are observed; when the buds reach a size between 4 and 6 mm they stop growing and enter dormancy. The breaking of dormancy is activated with the growth of the flower buds with their petals still closed. Following this phase, the anthesis, or opening of the flowers, occurs (Arcila et al., 2001). Flowering is a decisive phenological stage in the life cycle of the coffee plant (*Coffea arabica L.*) and is linked to crop production (Ramírez et al., 2010). This complex phenological process presents a marked interaction of environmental factors and physiological mechanisms that together condition the different stages of flowering development (Browning, 1973a).

Among environmental factors, temperature has various effects on the flowering stages of coffee plants, from flower induction to anthesis. Low temperatures are associated with the induction of flowering; therefore, flower buds can enter a dormant state during cold and dry periods. Temperatures of 23 °C during the day and 17 °C at night have been reported to be favorable for the synchronous development of flower buds in coffee plants. In contrast, temperatures higher than 30 °C during the day and 17 °C at night can inhibit flower initiation (Ramírez et al., 2010). Similarly, temperature, together with insolation and rainfall distribution, can influence the distribution patterns of flowering (Unigarro et al., 2023).

Water stress followed by rehydration has been identified as a trigger for flowering in coffee plants (Alvim, 1960; Astegiano et al., 1988; Santos et al., 2022). When plants are watered at short intervals such that the water content of the soil is close to field capacity, the flower buds remain dormant, and no fruits are formed, whereas flowering is induced by irrigation or rain only when it is preceded by a period of water shortage that induces water stress in the plant (Alvim, 1960; Ramírez et al., 2010).

At the endogenous level, an increase in the content of inhibitors in flower buds may be responsible for dormancy as a response to drought stress (Alvim, 1960). Water stress and subsequent rehydration are also associated with changes in ethylene synthesis and sensitivity (Lima et al., 2021; López et al., 2021). Ethylene biosynthesis is controlled by enzyme-encoding genes from multiple families, such as 1-aminocyclopropane-1-carboxylate synthase (ACS) and 1-aminocyclopropane-1-carboxylate oxidase (ACO), whose activity is influenced by water conditions (Lima et al., 2024). Gene expression has been shown to positively regulate ACO enzyme activity once the water supply is restored, contributing to increased ethylene production after rehydration (Lima et al., 2024). 1-Methylcyclopropene (1-MCP), an inhibitor of ethylene biosynthesis precursors, can promote flower bud development toward anthesis and even increase endogenous levels of ethylene in leaves and flower buds (Lima et al., 2024). Additionally, rain or irrigation modulates endogenous abscisic acid (ABA) levels, which increase during drought and decrease after rehydration; this modulation is possibly related to increases in ethylene levels and anthesis (Browning et al., 1970; Lima et al., 2024).

Aspects not yet addressed in studies on coffee flowering triggers, such as the physiological and functional traits of the plant, could facilitate understanding of the response to climate variability scenarios, as well as the ability of coffee species to acclimatize and adapt (Kasongi et al., 2024; Mamuye et al., 2024). Therefore, the objective of this systematic review (SR) was to analyze the progress of studies related to the main factors that promote coffee flowering, determine their relationship with production and identify the gaps that should be prioritized in future research. This SR focuses on the triggers of coffee flowering and synthesizes the main findings and current knowledge obtained through scientific publications over approximately 60 years, following the guidelines for systematic reviews.

2 Methodology

This systematic review was conducted in accordance with the guidelines of Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020) (Page et al., 2021) to elucidate the endogenous and environmental factors that trigger flowering in coffee plants. The protocol includes the determining the rationale, research questions, eligibility criteria, records to be examined and data synthesis for each study. The results revealed medium- and long-term effects on flower development, including the influence of temperature, photoperiod and water availability, as well as internal hormonal signals and gene expression.

2.1 Selection of scientific databases

Databases of private publishing clusters, such as *Science Direct*, *Taylor and Francis*, *Springer Link*, *Wiley* and *MDPI*, were included. In addition, a second group of databases considered large indexers was integrated: *Scilit*, *Dimensions*, *Web of Science*, *SciELO* and *EBSCOhost*. This diversification made it possible to cover both specialized resources and wide-ranging platforms in the academic community. The selection covered various types of scientific journals, including those classified as open access diamond (*diamond*), green (*green*), gold (*gold*) and hybrid, as well as publications with digital object identifier (DOI) identifiers that have not yet been indexed in recognized databases. This approach was based on a broad and representative coverage of studies related to the topic of interest.

2.2 Formulation of questions and selection of terms

Two questions were asked about triggers for flowering in coffee plants, with the main environmental variables separated from the endogenous variables. Similarly, the terms associated with each question were selected to address the variables in independent groups and facilitate the search for studies in scientific databases. To answer the question, "**What environmental factors trigger the flowering of coffee?**," groups of terms of the crop and phenological stages associated with climate and soil variables were used, including radiation, temperature, precipitation, relative humidity of the air and soil moisture:

1 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
2 ("solar radiation" OR "brightness" OR "sunshine" OR "shade" OR "insolation")
3 ("temperature" OR "atmospheric temperature" OR "thermal time" OR "thermal amplitude" OR "degree day")
4 ("soil moisture" OR "drought" OR "irrigation" OR "precipitation" OR "rain" OR "water stress" OR "water logging")
5 ("relative humidity" OR "atmospheric humidity" OR "vapor pressure deficit ")

Then, combinations of the first group of terms were used, with the other groups categorized, for a total of four combinations.

1 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("solar radiation" OR "brightness" OR "sunshine" OR "shade" OR "insolation")
2 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("temperature" OR "atmospheric temperature" OR "thermal time" OR "thermal amplitude" OR "degree day")
3 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("soil moisture" OR "drought" OR "irrigation" OR "precipitation" OR "rain" OR "water stress" OR "water logging")
4 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("relative humidity" OR "atmospheric humidity" OR "vapor pressure deficit").

Simultaneously, the following question was formulated**: What endogenous factors trigger the flowering of coffee?** The aim of this question was to integrate studies on genetic and physiological variables involved in coffee plant flowering. To answer this question, the following groups of terms of the crop and associated phenological stage were used, keeping the main group of terms related to the crop, the phenological stage of flowering and three more groups:

1 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
2 ("phytohormones" OR "ethylene" OR "abscisic acid" OR "gibberellic acid" OR "inhibitors" OR "nutritional status")
3 ("gene" OR "flowering locus" OR "homeologous regulation" OR "protein mediating" OR "orthologs")
4 ("growth plant" OR "stomatal changes" OR "ecophysiology" OR "CO_2 "OR "gas exchange")

The integration of the group of terms to answer the second question generated three combinations:

1 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("phytohormones" OR "ethylene" OR "abscisic acid" OR "gibberellic acid" OR "inhibitors" OR "nutritional status")
2 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("gene" OR "flowering locus" OR "homeologous regulation" OR "protein mediating" OR "orthologs")
3 ("coffee bloom" OR "coffee flowering" OR "coffee flower" OR "coffee flowers")
AND ("growth plant" OR "stomatal changes" OR "ecophysiology" OR "CO_2 "OR "gas exchange").

The search strategy in the scientific databases followed the specifications in Table 1.

2.3 Identification of the studies associated with each question

With the questions asked and each level of terms in the independent and combined groups, the respective searches were performed in the selected scientific databases. As a search filter, primary studies published in scientific articles were included, without limiting the coffee species, language or year of publication. Both indexed and nonindexed journals were included, along with references to some studies not identified via the search strategy, which were incorporated into the review. Three reviewers independently cross-checked the selection criteria and subsequently validated the extracted information. The number of studies for each scientific base was recorded in summary tables prepared in a spreadsheet, with the respective search date between October 15 and 25, 2024.

2.4 Debugging of duplicate studies

Once the studies associated with each question were obtained, duplicates were identified in the scientific databases through the downloading of the metadata for the studies in a spreadsheet, where the main indicator for debugging was the DOI code classification.

2.5 Selection of studies by relevance and association of terms in the title and abstract

The selected studies were imported into the Zotero bibliographic reference manager[1] to continue with the analysis of the metadata and the complete document in pdf format. This phase incorporated the assistance of ChatGPT 4.0 through prompts created with the objective of identifying the association of the terms in the title and the abstract; in addition, two evaluators (university students) under the supervision of a professional in library science performed the individual reading and verified the association of terms with the research questions formulated in the systematic review. The evidence for this procedure is reported at the end, in the Supplementary Datasets 1, 2.

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[1] https://www.zotero.org

TABLE 1 Search strategy for the scientific databases selected for the systematic review.

Database	Use of booleans	Website	Difficulties found	Solution
SCIENCE DIRECT	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	www.sciencedirect.com	Only up to eight Boolean connectors can be used (AND, OR and NOT)	Create a separate table, download the results and later validate the duplicates.
TAYLOR AND FRANCIS	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://www-tandfonline-com	None	
SCILIT	Supported Boolean operators AND, OR and NOT. No grouping in the same field	https://www.scilit.com/	You cannot perform an AND grouping search in a single search field.	To perform a grouping using the AND operator in the database, access the advanced search option. First, create a field where you will include the first group of terms. Then, add a second field, selecting the AND parameter to combine both groups. In this second field, enter the second set of terms. In this manner, the system will search for results that contain both groups of terms.
DIMENSIONS	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://app.dimensions.ai/	None	
SPRINGER LINK	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	link-springer-com	None	
WILEY	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://onlinelibrary.wiley.com/	None	
WEB OF SCIENCE	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://clarivate.com/academia-government/scientific-and-academic-research/research-discovery-and-referencing/web-of-science/	None	
SCIELO	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://search.scielo.org/	None	
EBSCO HOST	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses so that grouping is clear and unambiguous. (a OR b) AND (c OR d)	https://research-ebsco-com/	None	
MDPI	Supported Boolean operators AND, OR and NOT. Additionally, parentheses were used when nesting clauses to ensure clear and unambiguous grouping. (a OR b) AND (c OR d)	https://www.mdpi.com/search?	None	

2.6 Selection and eligibility criteria for studies

The eligibility criteria described in Table 2 were applied to each of the studies selected via the terms in the title and abstract, following the scientific structure of the text through the reading of the complete manuscript. Additionally, prompts were built to assist ChatGPT 4.0 in the synthesis of the information contained in the methodology and the results and in the verification by the related evaluators. Studies that met the eligibility criteria were included for the extraction of the information and the construction of the respective databases with the main findings. In addition, to identify each study, a consecutive numerical reference code associated with the DOI was assigned, available in Supplementary Datasets 1, 2.

2.7 Data extraction from studies selected by eligibility

To extract the data, a spreadsheet was constructed with fields to independently record the outstanding information for each study, including the reference number, DOI, author, year of publication, type of study, language, country of study, year of study and type of publication, among other factors. The assessment of individual risk of bias for each study included in the SR was based on a checklist with five domains, following the guidelines of the Cochrane Manual, which cover selection, performance, detection, attrition, and reporting bias. Each study was assessed by two independent evaluators for its methodology and results, using information extracted from previously prepared forms (Chandler et al., 2019).

2.8 Studies not recovered via the search strategy

The review of studies not identified via the standardized search strategy was carried out through repositories, printed documents or electronic downloads stored in institutional archives and some bibliographic references reported in the selected studies to integrate them into the results and discussion of the manuscript.

3 Results

The systematic review of studies on flowering in coffee plants revealed a relatively high concentration of research in Brazil ($n = 45$), followed by Colombia ($n = 38$), Ethiopia ($n = 12$), Costa Rica ($n = 10$), Mexico ($n = 10$) and Indonesia ($n = 9$) (Figure 1). Temporal analysis revealed a sustained increase in scientific production beginning in 2000, with 31 studies published between 2001 and 2010, 72 between 2011 and 2020 and 75 between 2021 and 2024 (Figure 2). With respect to the language of publication, 85% of the papers are in English, 12% in Spanish and 3% in Portuguese.

The overall risk of bias assessment in the systematic review showed: 83% of studies with a low risk, 10% with an uncertain risk, and the remaining 7% with a high risk, mainly due to data loss and selection bias. This information is detailed in the supplementary material (Supplementary Dataset 2). The validity of the results of the studies included in the SR demonstrates a low risk of bias, given the methodological rigor and quality of the analyses, which imply reliability in the findings.

From the analysis of the co-occurrence of terms in titles and abstracts related to studies on flowering in *Coffea arabica* and *Coffea canephora*, five thematic clusters were defined as follows:

- Blue cluster: genetic and physiological aspects, including terms such as *gene expression*, *floral induction*, *photoperiodism*, *abiotic stress* and *shoot apical meristem*, indicating interest in the molecular and regulatory mechanisms of flowering.
- Green cluster: environmental and climatic factors, such as *altitude*, *rainfall*, *climate* variability, *water stress* and *precipitation*, as well as management practices linked to agroclimatic conditions and crop modeling.
- Red cluster: biological and ecosystem interactions, focused on *pollination*, *Apis mellifera, native bees*, *shade-grown coffee*, *ecosystem services* and *biodiversity conservation*, reflecting the role of pollinators and biodiversity in coffee productivity.
- Purple cluster: physicochemical and quality properties linked to flowering and pollination, such as *monofloral honey*, *pH*, *moisture content*, *electrical conductivity* and *nectar*.
- Yellow cluster: finally, the integrative approach to cultivation, where *coffee flowering* acts as a central node that connects genetic, environmental, biological and management factors, highlighting the multidimensional complexity of the phenomenon.

Consequently, it is evident that flowering in coffee plants is a cross-cutting issue that integrates genetics with ecosystem interactions and the influence of climatic conditions and agricultural management (Figure 3).

3.1 Studies associated with environmental factors that promote flowering in coffee plants

Among the 706 studies retrieved by combining terms in the search strategy, 392 duplicates were identified; therefore, 314 were selected for further review. Of these, 68 included the term "coffee" with no relation to flowering, three addressed flowering with no link to coffee species, and 65 did not contain either term in the title and abstract. Consequently, 178 studies initially met the criteria of an association between coffee and flowering (Figure 4).

After the full evaluation of the documents, 135 were classified as unsatisfactory, while 43 met the eligibility criteria. Most of these studies focused on agroclimatic variables such as soil moisture, precipitation, temperature and sunlight (Figure 4). Additionally, 18 complementary studies were included and retrieved outside of the initial search strategy, which contributed to strengthening the results.

3.2 Description of the environmental determinants of coffee flowering

3.2.1 Soil-atmosphere hydric conditions

Coffee plant flowering presents different phenological stages determined by changes in the development of the nodes in the branches, such as bud swelling, differentiation, flower bud formation, dormancy, breaking dormancy and anthesis, which are associated with environmental factors (Arcila et al., 2001; Camayo et al., 2003). The distribution of dry and wet periods in the coffee regions of Colombia defines crucial moments for the growth of the coffee plant and the development of *C. arabica* crops (Jaramillo et al., 2011). The stress on the plant due to drought stops the growth of the floral structures and keeps them dormant; however, the intensity of the dry period can cause anomalies (Arcila and Jaramillo, 2003). If the condition of water stress is overcome with the application of irrigation

TABLE 2 Eligibility criteria of the studies for inclusion in the systematic review.

Section	Item	Compliance with criteria		Remarks
		Yes	No	
Title	The title addresses climate, soil or endogenous factors related to the flowering stages of coffee plants.	☐	☐	
Abstract	The structure of the abstract includes the synthesis of the background, method, results, discussion, conclusions and some climate, soil or endogenous factor(s) associated with the flowering stages of coffee plants.	☐	☐	
Methodology	**Inclusion criteria for the methods:** studies of coffee plants, flowering stages of coffee plants or climate, soil or endogenous variables; mentions the site where the study was carried out, type of study, experimental design, duration of follow-up, sample size, form of sample selection and type of analysis of the information. **Exclusion criteria:** studies of other crops or phenological stages other than flowering; does not provide information on the design, location, duration, sample size or analysis of the information.	☐	☐	
Results	The analysis of the information corresponds to the applied experimental design. Presents the estimates and significance values for the analysis. Reports the loss of information during the study. Reports whether they excluded data in the analysis.	☐	☐	
Conclusions	States that the conclusions correspond to the objectives set.	☐	☐	

or the beginning of the rains, the flower buds break the state of dormancy, and depending on the amount of water needed to meet the needs of the plant, the magnitude of flowering may vary (Ramírez et al., 2010).

Water stress is a fundamental requirement for coffee plant flowering *C. arabica* in equatorial or tropical regions since it allows the dormancy of flower buds to be broken. Subjecting coffee plants to continuous irrigation with soil moisture greater than 15% limited the opening of flower buds; in contrast, with soil moisture levels close to the wilting point (between 9.4 and 10.0%), abundant flowering occurred between 10 and 11 days after irrigation (Alvim, 1960). In the central coffee zone of Colombia, the formation of flower buds in *C. arabica* occurs mainly during the dry period between January and March, induced by anticyclonic conditions with high radiation and low humidity. Floral opening, or visible flowering, is promoted by the transition to the rainy period between March and June, when cloudy and cool days occur, stimulating the opening of flowers during the early hours of the day (Trojer, 1954b, 1956).

In agroforestry systems, the flowering of coffee *C. canephora* is determined by good infiltration and water availability in the soil after a dry period (Boreux et al., 2016). Specifically, anthesis promotion can occur after a precipitation event greater than 10 mm in a single day, preceded by a dry period, defined as an average rainfall of less than 0.6 mm for at least 11 consecutive days. Rain stimulates the breakdown of flower bud dormancy until anthesis is reached, at intervals of 7–10 days for *C. liberica*, 8–11 days for *C. canephora* and 10–14 days for *C. arabica* (Gomez et al., 2016). In addition, in *C. arabica* a large flowering event tends to occur more quickly (8–10 days) after a rain event than after a low-intensity event, which can take 10–13 days (Lara-Estrada et al., 2024).

The mobilization of water and calcium toward the flower buds is greater in *C. arabica* plants that have experienced a period of drought, which indicates that water stress facilitates the breakdown of dormancy; however, the underlying leaf in a node with inflorescences can increase the movement of water and calcium, and its absence does not prevent the breakdown of dormancy under stress conditions, suggesting a relative independence of the buds with respect to the leaf (Astegiano et al., 1988). In addition, water stress is considered a physiological trigger that eliminates growth inhibitors in the buds and may explain the flowering response (Alvim, 1960).

In terms of the reproductive dynamics of *C. arabica* plants under moderate or severe drought conditions, high CO_2 levels increase the number of reproductive structures and promotes their development, indicating greater reproductive effort as a survival strategy. During a period of atypical drought with respect to a normal climate, elevated CO_2 significantly reduces the proportion of floral structures with anomalies, which suggests the mitigation of the negative effects of high temperatures and water stress and improves flower induction as well as the quality of reproductive structures under environmental stress (Rakocevic et al., 2020). Otherwise, in scenarios with more frequent rainfall and less seasonality, a partial overlap in flowering periods has been determined between introduced coffee species, namely, *C. arabica, C. canephora* and *C. liberica*, associated with gene flow and interspecific hybridization between them (Gomez et al., 2016). The intensity of rains during flowering is associated with lower yields, causing scattered and smaller blooms and negative effects on pollination and fruit set (Guzmán and Baldión, 1999; Byrareddy et al., 2024).

To synchronize flowering and mitigate the bienniality of *C. arabica* production, the suspension of irrigation for a period of 70 days and subsequent rehydration led to a higher concentration of flowering, i.e., 84% of all flowers were open after ten days (Leite and Faria, 2016). Furthermore, both the optimization of irrigation and adequate fertilization are linked to greater floral emission and an increase in the number of fruits per branch (Boreux et al., 2016; Leite and Faria, 2016).

3.2.2 Thermal conditions (temperature - thermal units)

Temperature variations and accumulated thermal units (TUs) are determining factors in the phenological development of *C. arabica*, especially during the flowering and fruit development stages (Trojer, 1954a). Peters and Carroll (2012) reported flowering periods with temperatures between 20 and 26 °C, whereas Trojer (1954a) reported in *C. arabica* the development of flower buds at average annual temperatures from 17 to 23 °C, with differences between day and night temperatures of 5 to 7 °C, although it has been determined that

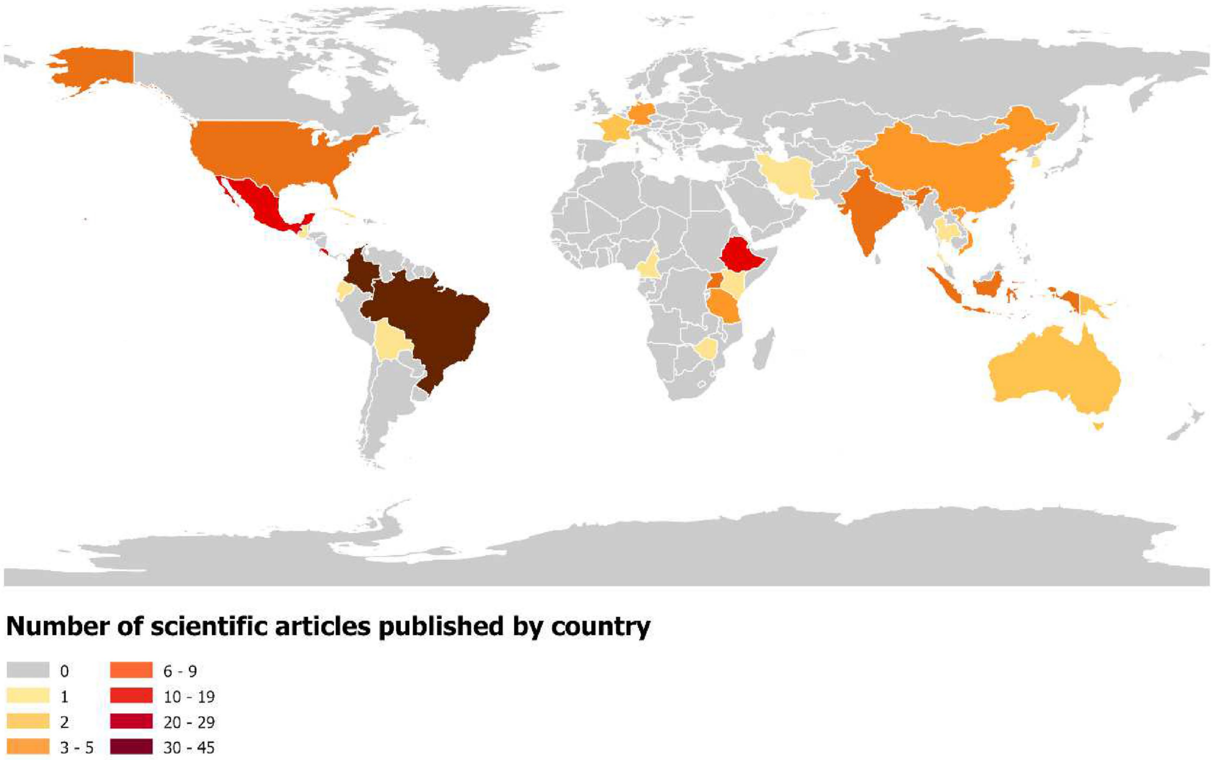

FIGURE 1
Scientific production by country according to the terms associated with the phenological stage of coffee flowering.

the minimum night temperature (Tmin) is the climatic factor that most affects flowering (Craparo et al., 2015). However, a lower temperature threshold of 10 °C and an upper threshold of 32 °C have been used to define the thermal units necessary for the speed of formation of vegetative and reproductive organs during coffee cultivation (Jaramillo and Guzmán, 1984).

For flowering, 3,250 accumulated TUs are necessary, with a base temperature of 10 °C, approximately 330 days from the sowing of the plant to six months of age (Jaramillo and Guzmán, 1984). Furthermore, Ramírez et al. (2010) explored the influence of the accumulated thermal time (TT) and observed a production of 1.4 flower buds/branch per 10-degree days of thermal accumulation.

Alterations in thermal dynamics have been shown to affect coffee plant flowering and production in *C. arabica* and *C. canephora* (Villers et al., 2009; Montoya and Jaramillo, 2016). In surveys conducted by Beristain-Moreno et al. (2024), coffee growers indicated the impact of the climatic variability observed since 2015 due to temperature extremes on the wide dispersion of the crop's flowering events. Similarly, in *C. arabica,* annual losses of 137 ± 16.87 kg ha^{-1} of green bean have been estimated in terms of coffee yields for each 1 °C increase in the minimum temperature (Craparo et al., 2015). For every 100 thermal units that are deficient or in excess of those needed, coffee production is decreased by 2.6% (Montoya and Jaramillo, 2016).

Shade trees can mitigate the extreme temperatures that affect the *C. arabica* crop, reducing the maximum temperature in the rainy season to between 3 and 6 °C and increasing the minimum temperature in the dry season to between 0.5 and 1 °C, with positive effects during the coffee flowering stage at sites that require agroforestry systems; however, because of its wide canopy density, the species *Cinnamomum camphora* (Lauraceae) can reduce coffee flowering by up to 50% (Rigal et al., 2020). Under this type of system, there is a general reduction in temperature of up to 2.5% with respect to the ambient temperature, which is considered important for avoiding the abortion of flowers caused by high temperatures (Coltri et al., 2019).

3.2.3 Luminosity (photoperiod - solar brightness - radiation)

Luminosity is a determining factor in the biological and physiological processes of plants, and the light absorbed by photosynthetic pigments uses energy and converts water and carbon dioxide into glucose and oxygen. Similarly, light influences the duration of phenological stages such as flowering (Castillo and López, 1966; Peña et al., 2011; Unigarro et al., 2023). According to Castillo and López (1966), the flowering of *C. arabica* is directly related to the amount of light received; as the light intensity increases, the number of buds per node increases, and the number of differentiated flowers in each bud increases.

The relationships between the length of the day, the photoperiod, and the flowering of coffee plants in different regions of Colombia indicate two types of floral patterns in the *Coffea arabica L.* species: annual (first photoperiod stage: November–April), with a shorter duration of the second stage of the photoperiod in the department of Cesar and continuous pattern in the departments of Cauca, Quindío and Caldas, affecting the dynamics of flowering (Unigarro et al., 2023). In turn, Peña et al. (2011) linked the photoperiod with the

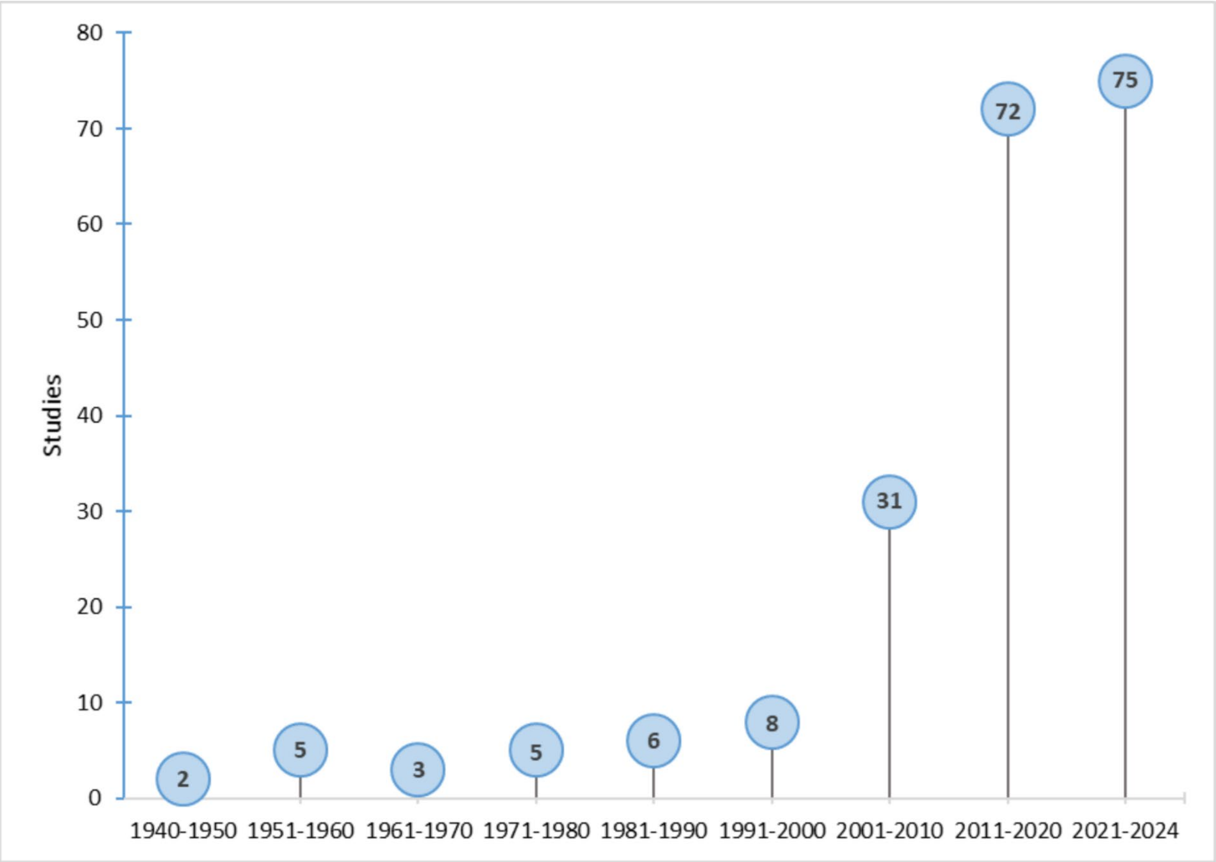

FIGURE 2
Number of studies retrieved according to the period of time in which they were published.

flowering process of the crop and found that shorter days (less than 13–14 h of light) two or three months before determine the induction of flowering in areas such as the departments of Cesar, Antioquia and Santander. Furthermore, in areas close to the equator, with latitudes close to 2° N, flowering is more strongly influenced by the duration of the days than by the soil water deficit.

3.2.4 Climate variability and change

The sensitivity of coffee plants to the variability of climatic elements such as temperature and precipitation affects the reproductive phases of flowering and fruit development (Villers et al., 2009). Variations in temperature, precipitation and vapor pressure deficit also affect phenology and yield in regions considered suitable for cultivation (Craparo et al., 2015; Mamuye et al., 2024; (Kasongi et al., 2024); Craparo et al., 2021).

Temperature is the climate variable with the greatest sensitivity in scenarios of climate variability and change (Villers et al., 2009; Gidey et al., 2020; Mamuye et al., 2024). Using data from a 40 and 49-year database, climate models constructed to estimate the increase in the maximum, minimum and average temperatures, indicate annual increases in the minimum temperature of 0.02 °C in Ethiopia (Mamuye et al., 2024), 0.042 °C in Tanzania (Kasongi et al., 2024) and 0.35 °C per decade in Tanzania, respectively, (Craparo et al., 2015), and annual increases in the maximum temperature of between 0.02 and 0.03 °C in Ethiopia (Mamuye et al., 2024); under the yield-SAFE model, an increase in the average temperature between 1.1 and 3.1 °C is estimated for the year 2050 in Ethiopia (Gidey et al., 2020), while Villers et al. (2009) estimated annual increases in the mean temperature of up to 2.7 °C in Mexico, based on 30 years of data under the GFDL-R30 and CCCM models.

Precipitation models estimate annual increases or lags that can affect coffee plant flowering (Villers et al., 2009; Byrareddy et al., 2024; Mamuye et al., 2024). Using a series of climate data from more than 40 years, Mamuye et al. (2024) observed a trend with increases in average annual precipitation between 5.09 and 6.49 mm. Under the CCCM model with a base of 30 years, Villers et al. (2009) forecast variations each year close to ± 500 mm, whereas under the GFDL-R30 model, an increase of 52 mm is expected during the dry period in Mexico, which may affect the necessary stimulus of water stress for flowering during the first semester for both *C. arabica* and *C. canephora*. In contrast, the prediction of the CCCM in a scenario of prolonged drought for a period of four months, with an average of 45 mm, can limit the water requirements for coffee flowering. Changes in precipitation during the flowering season of *C. arabica* are important, and the dispersion, decrease or increase in rainfall directly influences the timing of this phenological stage and the quality of the grain (Craparo et al., 2015). Similarly, climatic conditions with high-intensity rains greater than 100 mm during the flowering period directly affect yield of *C. canephora* crop (Byrareddy et al., 2024).

Variations in temperature impact the development of blooms and the production of the coffee crop; if the trend of increasing

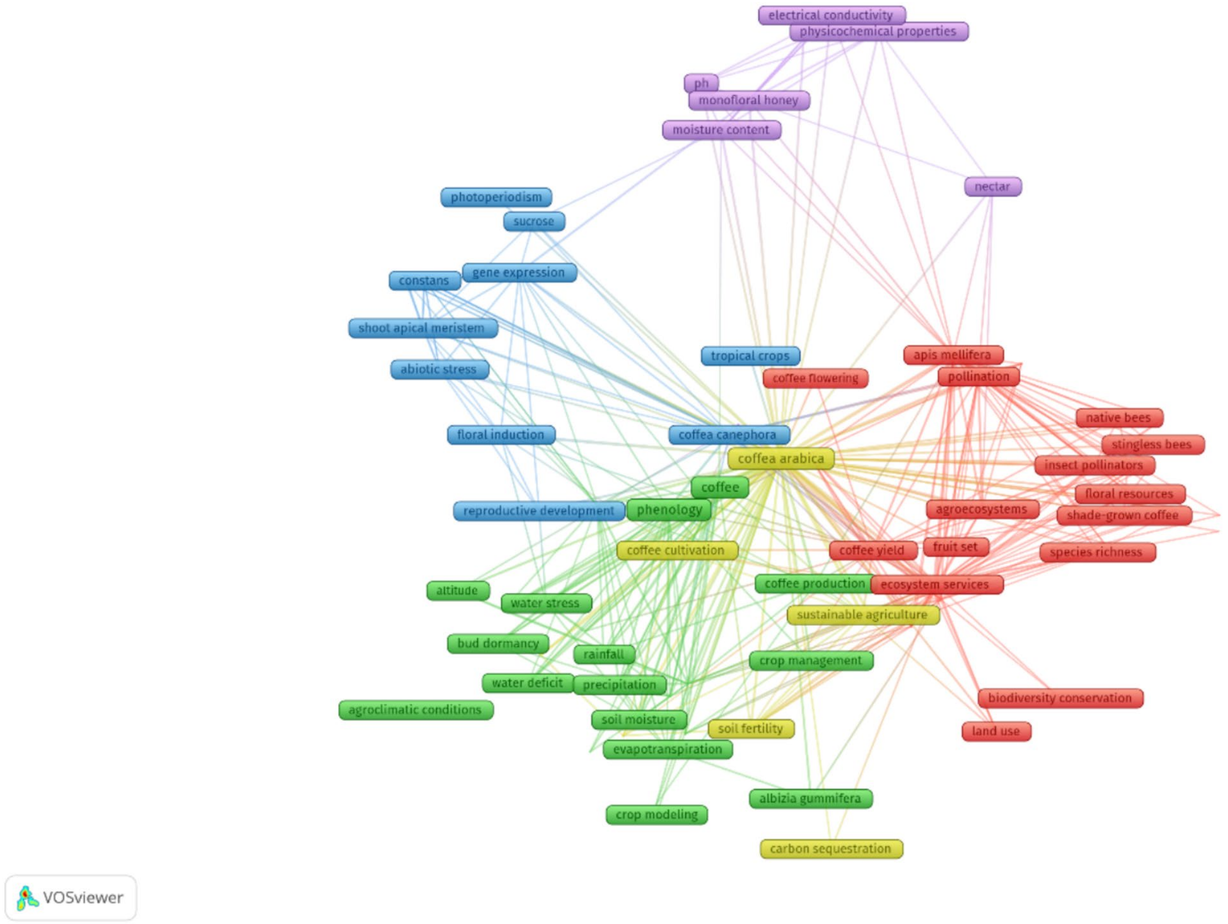

FIGURE 3
Network map based on the co-occurrence of terms in the title and summary associated with the phenological stage of coffee flowering, created using VOSviewer.

the minimum temperature is maintained, the average production of green coffee of *C. arabica* may decrease by 2060 to 145 ± 41 kg ha^{-1} (Craparo et al., 2015). Night temperatures are also predominant in the flowering and ripening of fruits, so the warm night indices (WNIs) based on the average night temperature explain up to 95% of the variability at the beginning of the harvest. Furthermore, for every 1 °C increase in the WNI, the harvest can be early by approximately 17 ± 1.95 days (Craparo et al., 2021). The sensitivity of robust coffee plants to climatic stress is specifically associated with early blooms when there are warmer minimum temperatures, lower maximums, greater precipitation and a shorter duration of the dormancy period (Kath et al., 2023).

As a consequence of climate change, areas traditionally considered suitable for coffee cultivation may lose their suitability by 2064 (Kasongi et al., 2024). To address this situation, adaptation strategies for growing coffee plants have been proposed (Villers et al., 2009). One of the most commonly used methods is the establishment of the crop under shade or agroforestry systems (Lin and Richards, 2007; Boreux et al., 2016; Coltri et al., 2019; Rigal et al., 2020). The transition from monoculture to agroforestry systems provides microclimate benefits by mitigating extreme conditions (Rigal et al., 2020). Lin and Richards (2007) reported that the average shade levels (30–50%) typical of agroforestry systems lead to the greatest efficiency, capturing up to 28% of precipitation in regions with water limitations.

In agroforestry systems with coffee, shade trees can reduce water and heat stress, in addition, by improving water infiltration into the soil, can promoting the breakdown of the dormancy of flower buds (Boreux et al., 2016). This finding is consistent with that reported by Coltri et al. (2019), where the temperature in the shade is reduced by 0.63 °C compared with the system in full sun, the wind speed is reduced up to 99.3%, and the relative humidity is increased during the driest periods. With respect to the vapor pressure deficit (VPD), at low-altitude sites, the optimum value of 0.82 kPa for coffee productivity has been exceeded since 2023, whereas at intermediate altitudes for cultivation, this value is expected to be exceeded in the mid-2040s (Kasongi et al., 2024).

Based on the knowledge of the environmental factors linked to the expression of the main phenological stages of coffee cultivation, models have been constructed to predict floral events from simple climatic data to facilitate agricultural planning, such as the strategic use of irrigation and the design of index-based insurance to mitigate risks from extreme rains during flowering (Beristain-Moreno et al., 2024; Lara-Estrada et al., 2024). By way of synthesis, Table 3 presents the studies of the main environmental variables

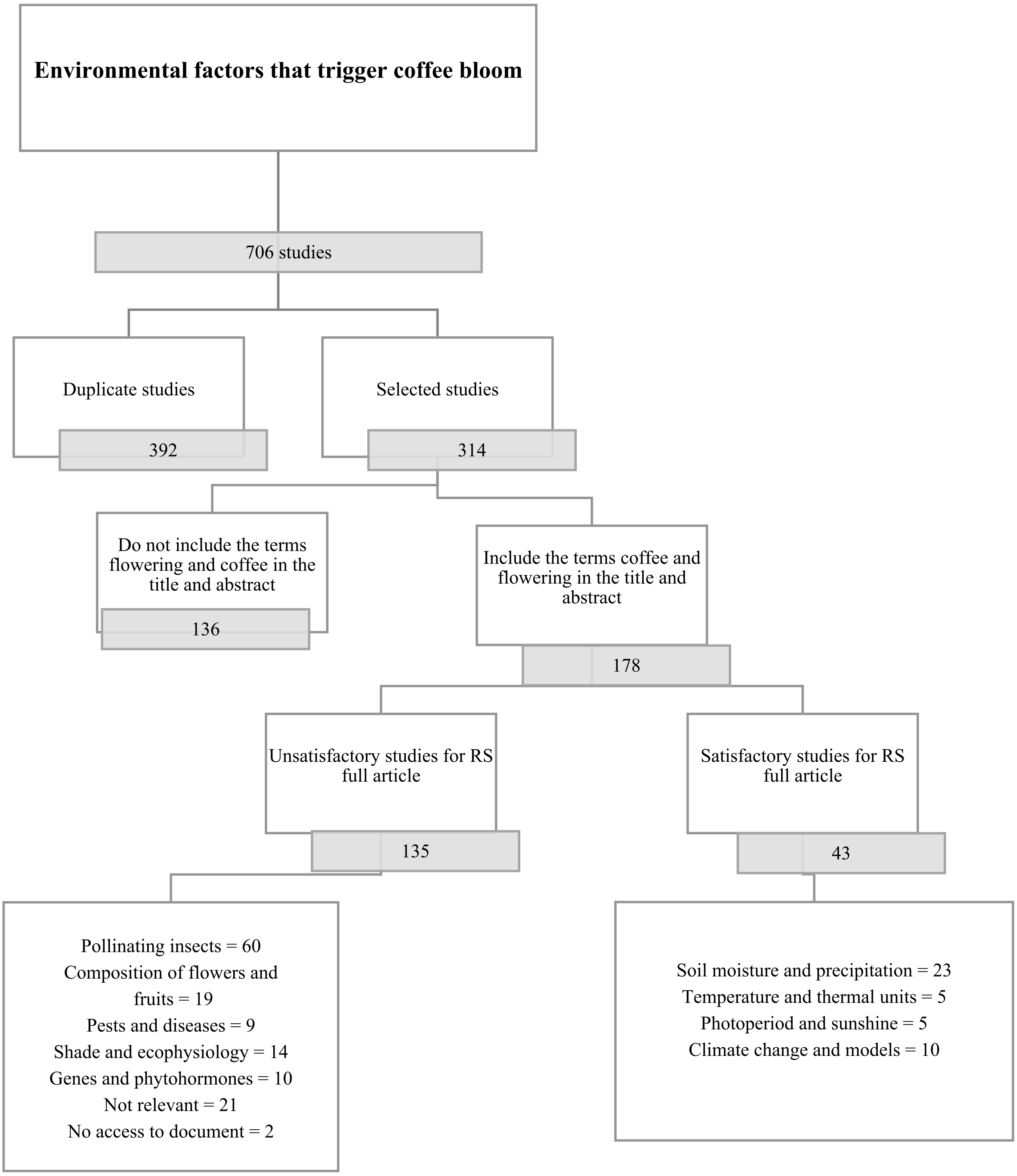

FIGURE 4
PRISMA flowchart for selecting studies on environmental factors associated with coffee flowering.

associated with coffee flowering that were identified via the systematic review strategy.

3.3 Studies associated with endogenous factors that promote coffee flowering

Among the 187 studies retrieved by combining terms in the search strategy, 55 duplicates were identified, leaving 132 for review. Of these, 23 included the term "coffee" unrelated to flowering, 33 were not associated with coffee species, and 76 presented a direct association between coffee and flowering (Figure 5).

After full evaluation of the studies, 53 were classified as unsatisfactory, while 23 met the eligibility criteria. Most of these studies focused on genetics and phytohormones (Figure 5). Additionally, nine complementary studies were included that were identified outside the initial search strategy but contributed relevant evidence to the results.

3.4 Description of the endogenous determinants of coffee flowering

3.4.1 Gene contribution

Knowing the role of gene expression in the reproductive processes of coffee cultivation is of interest for understanding the response of plants during different stages of phenological development (Silva et al., 2021) and the relationship with biosynthesis and environmental stimuli (Browning et al., 1970; Mohan Ram and Rao, 1984; Lima et al., 2021, 2024). Based on the evidence from the cited research, the genes that are associated with coffee plant flowering include the MADS-box "minichromosome maintenance protein 1, agamous, deficient, serum response factor"; ACS "1-aminocyclopropane-1-carboxylic acid synthase"; ACO "1-aminocyclopropane-1-carboxylic acid oxidase"; *FT* "*FLOWERING LOCUS T*"; and *FD* "*FLOWERING LOCUS D*" genes.

3.4.1.1 MADS-box

In the MADS-box gene family, type II (MIKC) genes stand out for their role as regulators of reproductive development, the identity of floral organs and the determination of the floral meristem (De Oliveira et al., 2014; Rume et al., 2023). Otherwise, the expression of the *FLOWERING LOCUS C (FLC)* gene preserves the MADS-box domain and is related to the regulation of flower induction time, in addition to environmental conditions such as prolonged water stress (90 days), which is considered a key factor in triggering flowering, as the *CaFLC-like* gene is expressed at its highest level in the flowers and leaves of flowered branches. Other genes involved in the regulation of flower induction time are *COS1*, *AGL19* and *AGL14* under different environmental conditions (Barreto et al., 2012; Rume et al., 2023).

CaAP1/CAL, *CaAP3*, *CaPI* and *CaAG* gene expression patterns are present in all stages of flower organ formation, unlike *CaTM6*, whose expression is absent during the initial stages. In turn, the *CaAP1/CAL*, *CaAP3* and *CaTM6* genes are expressed first in the internal bracts and the meristem and later in the petals and sepals, whereas *CaPI* and *CaAG* are expressed in vascular bundles and organs such as the meristem, stamens and carpels (De Oliveira et al., 2014).

3.4.1.2 ACS-ACO

The ACS and ACO gene families show organ-specific expression patterns according to the water conditions of the plant. When a plant is under water deficit conditions, *CaACS3* expression increases in open flowers; *CaACS1*, *CaACS3* and *CaACO4* expression increases in flower buds (Santos et al., 2022); and *CaACO1-like* expression increases in leaves and roots, which implies modifications in the metabolic pathways of ethylene synthesis (Lima et al., 2021). Another study reported that *CaACS1* and *CaACO4* do not present relevant changes in response to water deficit (Lima et al., 2021).

3.4.1.3 Ft-FD

FT promotes the conversion of the apical stem meristem (SAM) into inflorescence meristems (López et al., 2021). In coffee, the expression of florigen *CaFT1* peaks under low temperatures and a short photoperiod; in addition, its expression is potentiated when high levels of total soluble sugars are present, which suggests a relationship between sugar metabolism and the function of florigen in coffee plants (Cardon et al., 2022). Similarly, *FD* and *14–3-3* are transcription factors that activate flowering identity genes such as *SOC1*, *APETALA 1 (AP1)* and *FRUIT FULL (FUL)* (López et al., 2021). The expression of *14–3-3* is stable during the flowering stage, with small variations during flowering stage initiation (Barsalobres-Cavallari et al., 2009).

3.4.1.4 Morphological traits associated with genotypes

Flowering and its morphological traits are related to coffee genotypes and the interactions with environmental factors. The contribution of the morphological traits of flowering determined by genotype can explain the genetic diversity in characteristics such as style length, corolla tube and stigmatic lobe (39.8, 22.4 and 12.7%, respectively) (Silva et al., 2021). In addition, the length of the tube, the number of floral appendages and the diameters of the corolla and pollen tube can explain up to 70.8% of the observed phenotypic variability (Silva et al., 2024a).

A predominant feature of *C. arabica* is the occurrence of pentameric flowers, whereas *C. canephora* tends to present flowers with six floral appendages (Silva et al., 2024b). Under shade, the flowers of *C. arabica* are characterized by a greater corolla diameter (1.4%) and a longer staminal filament length (12.8%). On the other hand, *C. canephora* flowers are characterized by a greater pollen tube length (8%) and a greater corolla diameter (3.7%). In contrast, free sun exposure for *C. canephora* results in a symmetrical increase in most flower traits, and for *C. arabica*, only the increase in the length of the pollen tube is relatively greater (8%) (Prado et al., 2019). Another interaction of the environment that results in larger floral structures is the altitude at which the crop is established (Silva et al., 2024b).

3.4.2 Phytohormone activity

Coffee anthesis occurs under conditions of water deficit followed by rehydration, involving the coordinated action of phytohormones such as ethylene, ABA, and gibberellins during developmental stage transitions, together with gene interactions, as reported by López et al. (2021) and Lima et al. (2024). An examination of the mechanistic contributions of each hormone, as well as other compounds involved in the control of coffee anthesis, is presented in the following sections.

3.4.2.1 Ethylene

Ethylene dynamics in coffee are tightly regulated by water availability and rehydration cues. Under water-deficit conditions, ethylene biosynthesis is suppressed in both vegetative and reproductive tissues, maintaining floral bud dormancy (Lima et al., 2021). Upon rehydration, ethylene levels increase four- to twelvefold in the leaves, coinciding with enhanced expression of *CaACO1-like*, a key gene involved in ethylene biosynthesis in roots and leaves. The reactivation of the ethylene pathway triggers downstream signaling events that facilitate the transition from dormancy to anthesis. Exogenous application of 1-MCP, an inhibitor of ethylene perception, can induce anthesis in the absence of rehydration, indicating that inhibition of ethylene signaling is sufficient to release floral buds from dormancy. This treatment also alters the transcriptional profiles of ethylene receptor genes (*CaERS1-like*, *CaETR2-like*, *CaETR4-like*, and *CaEIN4-like*), reducing their expression in buds while concomitantly increasing *CaACO3-like* activity (Lima et al., 2024), thereby suggesting the existence of a feedback mechanism between ethylene signaling and biosynthesis during anthesis induction.

The regulatory role of ethylene in this process appears to be closely coordinated with other hormonal pathways. Ethylene-mediated signaling may interact with abscisic acid (ABA) to modulate the

TABLE 3 **Summary of key findings on the environmental triggers of coffee flowering.**

DOI (year) Ref	Country	Study type	Variables	Treatments	No. of repetitions	Sample size	Effects on flowering
Soil moisture							
10.1016/j.pce.2009.06.013 (2009)[001]	Zimbabwe	Inferential	Soil moisture	3	9	27	The application of 25 liters of water per tree led to an amount of 96.3 flowers per branch, when irrigation was programmed at 20 cb.
10.1007/s13593-016-0377-7 (2016)[029]	India	Observational	Soil moisture	112	10		The superficial tillage of the soil favors flowering by improving infiltration after a dry period.
10.1080/14620316.1988.11515888 (1988)[105]	Brazil	Inferential	Soil moisture				The water uptake of flower buds in stressed plants reaches values of 4521.92 dpm μg^{-1} DM at a water potential of −23.0 MPa, compared to 119.28 dpm μg^{-1} DM in plants not stressed at −0.3 MPa.
10.1007/s00344-024-11481-x (2024)[107]	Brazil	Inferential	Soil moisture	2	4		An initial endogenous level of ethylene of 2 ppm g^{-1} FW h^{-1} in flower buds increases after the application of 1-MCP up to 10 ppm g^{-1} FW h^{-1}; if irrigation is applied, the production of ethylene is reduced at 1 ppm g^{-1} FW h^{-1}.
10.1007/BF00024674 (1994)[123]	United States	Observational	Soil moisture				The breaking of the dormancy of the flower buds when retaining water leads to increases of 5 and 9% in the fresh and dry weight, respectively, between 3 and 5 days after rehydrating the plants.
10.5892/ruvrd.v14i1.2937 (2016)[144]	Brazil	Inferential	Soil moisture	4	3	36***	The suspension of irrigation for 70 days favors a greater concentration of flowering, with 84% of the flowers opening completely, 10 days after restarting the irrigation.
10.1126/science.132.3423.354 (1960)[145]	Peru	Observational	Soil moisture	2	10		Soil moisture above 15% in coffee plants subjected to weekly irrigation prevents the opening of flower buds. In contrast, in plants that reach a soil moisture of between 9.4 and 10%, flowering occurs 10 to 11 days after irrigation.
SINDOI-Cenicafe-19 Ramírez et al. (2010)[170]	Colombia	Observational	Soil moisture			7**	With a WAI < 0.3 in the central coffee zone of Colombia, 2,546 flower buds/180 branches were recorded per event.
10.1016/j.agwat.2007.05.014 (2007)[009]	Mexico	Observational	Precipitation	2	20		A level of shade between 30 and 50% presents greater efficiency in capturing the precipitation required to promote anthesis.
10.1016/j.ecoinf.2023.102434 (2024)[057]	Nicaragua	Inferential	Precipitation		4	53*	A high-intensity flowering event tends to occur more quickly (8 to 10 days) after a rain event ≥ 10 mm compared to a less intense flowering event (10 to 13 days).
10.1002/ece3.2055 (2016)[060]	France	Observational	Precipitation	367	10	30	Anthesis occurs after a precipitation event greater than 10 mm in a single day, provided that it is preceded by a period of at least 11 consecutive days without rain.
SINDOI-2 Villers et al. (2009)[083]	Mexico	Observational	Precipitation			30*	The GFDL-R30 model predicts a reduction in the drought period from 4–2 months (February–March), with an increase in precipitation (52 mm), which may limit the stimulus needed to promote high-magnitude blooms.
10.1016/j.envc.2024.100950 (2024)[065]	Ethiopia	Observational	Precipitation	3**		42*	Significant trends are identified in the increase in precipitation, with average annual rates between 5.09 and 6.49 mm; these increases have implications in the different phenological stages of the crop.

(Continued)

TABLE 3 (Continued)

DOI (year) Ref	Country	Study type	Variables	Treatments	No. of repetitions	Sample size	Effects on flowering
Thermal conditions							
10.1016/j.agsy.2019.102696 (2020)[008]	China	Observational	Temperature	2	20	3**	Shade trees provide microclimatic benefits by mitigating extreme temperatures by reducing the maximum between 3 and 6°C; proper management of the shade level favors the conditions for flowering.
10.1016/j.agrformet.2015.03.005 (2015)[005]	Tanzania	Observational	Temperature			49*	The flowering of coffee plants is negatively affected by the increase in the minimum temperature; according to this analysis, increases of 0.35 °C per decade are estimated during the flowering period.
10.1016/j.envc.2024.100950 (2024)[065]	Ethiopia	Observational	Temperature	3**		42*	Significant trends are identified in the increase in temperature, with average annual rates of 0.02 °C in the minimum temperature and between 0.02 and 0.03 °C in the maximum temperature and negative effects on the development of flower buds.
SINDOI-Cenicafe-7 Jaramillo and Guzmán (1984) [158]	Colombia	Observational	Thermal units			47	For the first coffee plant flowering to occur, approximately 3,250 thermal units are required, and 330 days elapse after sowing in the field.
SINDOI-Cenicafe-19 Ramírez et al. (2010)[170]	Colombia	Observational	Thermal units			7**	The influence of TT on flowering in the central coffee zone of Colombia under the applied regression model estimates between 25 and 40 flower buds/180 branches for each degree day of thermal accumulation.
Photoperiod							
10.3390/plants12183332 (2023)[134]	Colombia	Observational	Photoperiod			8**	Blooms concentrated in a single half of the year are related to a reduction of more than 30 min in the length of the day.
SINDOI-Cenicafe-1 Peña et al. (2011)[142]	Colombia	Observational	Photoperiod		30	8**	The most important flowering periods are related to short days (less than 13 or 14 h of light).
SINDOI-Cenicafe-6 Castillo and López (1966) [157]	Colombia	Observational	Sunshine	4	2	8	At light intensities of 25 and 100%, there are between two and four glomeruli per node, respectively.

* years, ** locations, *** plots. Units and acronyms in the table. cb = centibar, dpm μg^{-1} DM = decays per minute per microgram of dry matter, MPa = megapascals, WAI = water availability index, TT = accumulated thermal time, 1-MCP = 1-methylcyclopropene, ppm g^{-1} FW h^{-1} = fresh weight per hour, ACC = 1-aminocyclopropane-1-carboxylic acid.

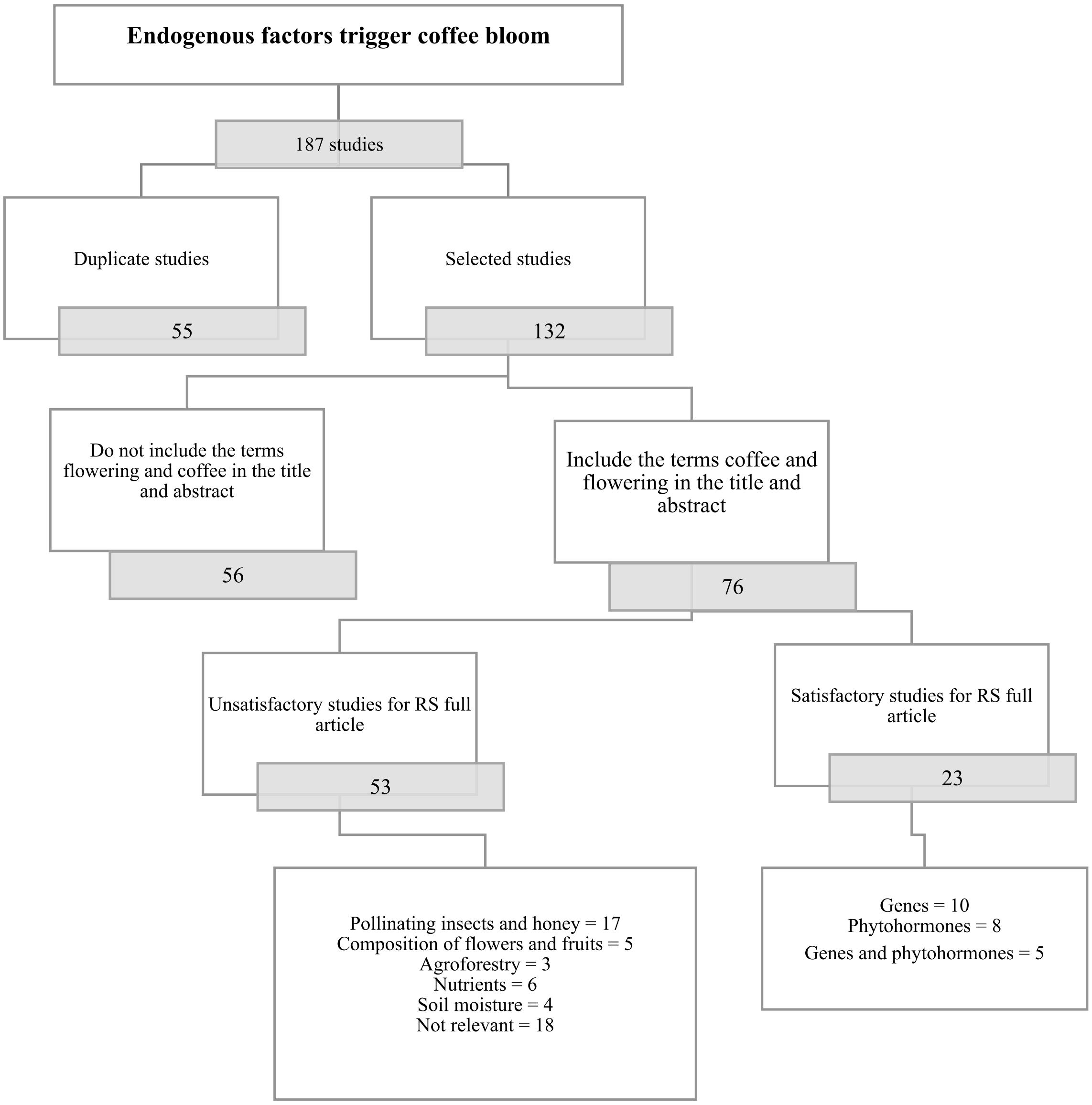

FIGURE 5
PRISMA flowchart of the selection of studies on endogenous factors associated with flowering in coffee plants.

maintenance and release of floral dormancy under drought conditions, while its reactivation upon rehydration likely facilitates gibberellin (GA)-dependent processes that promote floral organ development and anthesis. Recent findings further support this integrative view, showing that exogenous applications of GA and ABA during both floral induction and bud development significantly increased the number of floral buds and accelerated their development, suggesting a synergistic rather than purely antagonistic interaction between these hormones in coffee (Azevedo et al., 2025). These interactions underscore a complex hormonal network that integrates environmental cues with endogenous signaling to finely regulate coffee flowering.

3.4.2.2 Abscisic acid (ABA)

The resumption of flower growth in coffee is tightly regulated by abscisic acid (ABA) dynamics within the floral bud. Under water-deficit conditions, elevated ABA levels maintain dormancy through the repression of growth-promoting processes. Following rehydration, ABA concentrations in the buds decline sharply, coinciding with a reduction in growth-inhibitory activity and the activation of promoters of cell expansion and differentiation (Mohan Ram and Rao, 1984; Lima et al., 2024).

Quantitatively, ABA levels decrease from approximately 0.1–0.16 μg g^{-1} dry weight in dormant buds to 0.04–0.09 μg g^{-1} in active buds, reflecting an inverse and antagonistic relationship between ABA accumulation and floral activation (Browning et al., 1970). This decline in ABA likely represents a key regulatory signal that releases buds from dormancy, enabling the subsequent activation of ethylene- and gibberellin-dependent pathways associated with anthesis progression. Nonetheless, more recent studies challenge the traditionally inhibitory view of ABA in flowering regulation. A 2025 study demonstrated that ABA applied at 25–100 ppm during both the floral induction (March) and bud development (August) stages significantly increased the number of floral buds and even accelerated their development, mirroring the promotive effects observed with gibberellic acid (GA) treatments. Moreover, molecular analyses revealed that these hormones modulate the expression of genes involved in floral induction and organ formation, suggesting that ABA may act as a positive regulator under specific developmental contexts (Azevedo et al., 2025).

3.4.2.3 Gibberellins

Gibberellins play a central role in reactivating flower development following rehydration. A rapid increase in gibberellin levels within two days of rehydration represents a key signal for the resumption of floral growth. In contrast, gibberellin concentrations in the xylem sap remain stable, suggesting that the active hormone pool originates locally within the buds rather than being transported from the roots (Browning, 1973a). This localized activation of gibberellin biosynthesis likely contributes to the reinitiation of cell expansion and differentiation processes in floral tissues. Furthermore, gibberellins appear to enhance cytokinin accumulation in buds following rehydration after prolonged drought, indicating a coordinated hormonal response that links floral induction to the alleviation of water stress (Browning, 1973b).

Crosstalk between gibberellin and jasmonate signaling pathways also contributes to the fine regulation of floral development. Jasmonates can antagonize gibberellin signaling, and the synthesis of methyl jasmonate in floral tissues suggests a specialized role in modulating flower-specific processes, including the regulation of the *FatB* gene involved in fatty acid biosynthesis (Privat et al., 2011). Such interactions indicate that lipid metabolism may be functionally integrated into the hormonal control of anthesis.

Exogenous application studies further support the promotive role of gibberellins in coffee flowering. Treatment of *C. arabica* buds larger than 4 mm with 100 mg·L^{-1} gibberellic acid (GA_3) induces anthesis up to 20 days earlier than in untreated plants, independent of water status, leading to more synchronized fruit ripening in Hawai (Schuch et al., 1990). However, other experiments have shown limited or no enhancement in floral bud formation or yield when GA_3 and potassium nitrate (KNO_3) are applied during the knot induction stage, in the central coffee-growing region of Colombia (Unigarro et al., 2019), suggesting that the effectiveness of exogenous GA_3 depends on the developmental stage and hormonal context of the buds. Recent evidence supports this interpretation, as applications of GA at 5–100 ppm during both floral induction and advanced bud stages significantly increased floral bud number and fruit production, and altered the expression of genes associated with floral induction and organ formation (Azevedo et al., 2025).

3.4.2.4 Auxins

Auxin dynamics also play an important role in regulating coffee anthesis following rehydration. Levels of indole-3-acetic acid (IAA) rise markedly within one day of rehydration, reaching approximately 60% of the total IAA content per bud and 41% of the pre-anthesis level before the onset of accelerated floral growth (Schuch et al., 1994). This transient increase suggests that IAA participates in the early stages of bud reactivation, possibly by promoting cell expansion and vascular reconnection within the developing floral tissues. However, exogenous application of IAA delays floral induction by extending the flower initiation period to about 25 days, indicating that excessive auxin accumulation may reinforce inhibitory feedback mechanisms that maintain bud quiescence.

Similarly, application of the synthetic auxin 2,4-dichlorophenoxyacetic acid (2,4-D) exerts dose-dependent effects on floral development. Treatments with 100 ppm prolong flower formation for approximately 20 days, and the localized action of 2,4-D restricted to treated plagiotropic branches without translocation to adjacent tissues demonstrates the spatial specificity of auxin signaling in coffee (Cueto and Dathe, 1986). These findings support the notion that fine-tuned regulation of auxin gradients, rather than overall concentration, is critical for coordinating floral initiation and development after rehydration.

A summary of the main functions of phytohormones and environmental triggers involved in coffee plant flowering is presented in Table 4.

3.4.2.5 Other compounds present in flowering coffee plants

The reactivation of metabolic pathways during flowering not only supports reproductive development but also contributes to the biosynthesis of volatile and specialized metabolites that define coffee quality. In the early stages of flower and fruit development—approximately 10 and 15 weeks after pollination, respectively—monoterpene synthase activity is elevated, leading to the predominant accumulation of linalool and β-myrcene, compounds that play a central role in floral aroma formation (Del Terra et al., 2013). During flowering and grain formation, diterpene biosynthesis is also intensified, with cafestol (CAF) and kahweol (KAH) reaching concentrations of approximately 263.75 mg per 100 g fresh weight in flower buds and 1009.48 mg per 100 g in the perisperm 120 days after flowering, respectively (Ivamoto et al., 2017). These data indicate that the activation of terpene metabolic pathways is closely associated with the differentiation of floral and fruit tissues.

Nitrogenous secondary metabolism likewise undergoes reprogramming during anthesis and early fruit set. Caffeine biosynthesis intensifies in prefruiting stages, coinciding with the highest accumulation of theobromine in the gynoecium, while caffeine predominates in flower buds and theophylline accumulates in petals (Montis et al., 2024). This tissue-specific distribution suggests dynamic regulation of purine alkaloid metabolism, in which caffeine catabolism in the petals may contribute to modulating energy balance and developmental signaling during flowering.

3.4.2.6 Nutrients

Nutrient allocation and uptake represent key regulatory components of coffee reproductive development and are strongly influenced by genotypic variability. Genetic background determines both the intensity and timing of nutrient demand, particularly during the pre-flowering and bean-filling stages, when active metabolic and biosynthetic processes require increased nutrient flux (Gomes et al., 2016). Among characterized genotypes, Verdin R and Pirata exhibit significantly higher concentrations of macro- and micronutrients in floral tissues compared with Bamburral, A1, P1, Verdin TA, and NV2, suggesting greater nutrient acquisition efficiency or preferential allocation to reproductive organs (Santos et al., 2021).

The nutritional composition of flowers also provides valuable insight into plant physiological status. Because floral nutrient levels remain more stable than those in leaves, flower tissue analysis has been proposed as a reliable diagnostic tool for early nutritional assessment. Strong correlations have been reported between floral and foliar concentrations of nitrogen (N), phosphorus (P), calcium (Ca), iron (Fe), copper (Cu), and manganese (Mn), highlighting the potential of reproductive tissues as sensitive indicators of nutrient availability and mobilization within the plant (Zabini et al., 2021). These findings underscore the mechanistic link between nutrient homeostasis, reproductive development, and the broader metabolic network supporting anthesis and fruit initiation.

Table 5 presents the results of the studies of the main endogenous factors associated with coffee plant flowering that were identified via the systematic review strategy.

4 Discussion

Systematic review through the proposed strategy allowed the identification of a greater number of studies that associate water availability in the soil as a determining environmental factor for the flowering stage in coffee. A foliar water potential of −1.2 MPa followed by the application of irrigation significantly increased the percentage of open buds and concentrated the flowering into one event or in several events that exceeded 60% of the opening of the flower buds. However, to reach this water potential, a duration without the application of irrigation of more than 70 days and rehydration with volumes equivalent to a precipitation greater than 35 mm were required (DaMatta et al., 2007; Morais et al., 2008; Miranda et al., 2020; Ronchi and Miranda, 2020).

On the other hand, water deficit levels between −0.59 and −0.82 MPa are not enough to superimpose the effect of rain on flower opening; consequently, continuous irrigation leads to fewer flowers and a lower temporary concentration (Silva et al., 2009; Ronchi et al., 2015). When the decrease in the leaf water potential reaches −1.87 MPa, a logarithmic increase in flowering occurs (Ronchi and Miranda, 2020). In contrast, Crisosto et al. (1992) reported floral synchronization with periods of moderate deficit persisting for at least two weeks. Although uniform development of the inflorescences in dormancy prior to hydric sufficiency is essential for abundant blooms, the opportune timing of irrigation is also important for inducing anthesis (Drinnan and Menzel, 1994; Soares et al., 2005).

The findings concerning temperature reveal higher values of accumulated thermal units (GDD) during the flowering period under conditions of moderate water availability, with more concentrated and anticipated blooms (da Silva Angelo et al., 2019). There is a greater number of inflorescences per node with temperatures between day and night of 23 °C and 18 °C, respectively (Drinnan and Menzel, 1995). The temperature threshold to activate or stop flower anthesis is 12.9 °C and 32.4 °C, respectively. On the other hand, a base temperature of 10.2 °C and requirements between 2,887 and 4,200 GDD promote the synchronization of flowering (Lima and Silva, 2008; Pezzopane et al., 2008).

Water availability and temperature are related to luminosity and are considered parameters that define the establishment of production systems in the sun or under shade during coffee cultivation (Jaramillo and Chaves, 1999). In places with high levels of solar radiation, during the initial stages of coffee plant flowering, shade levels between 50 and 70% anticipate the differentiation of flower buds, whereas under free solar exposure, flower bud differentiation can take approximately 1 month (Queiroz et al., 2011).

Faced with climate challenges, the application of agrometeorological models contributes to the identification of weather patterns, extreme conditions and their relationships with phenological stages. Models that identify extreme minimum temperatures and prolonged water deficit during the period of flower induction and flowering have revealed a significant effect on coffee productivity (Santos and Camargo, 2006). Through these models, a cumulative value of potential evapotranspiration (ETp) of 335 mm, which is associated with a minimum precipitation of 7 mm, represents the best combination to induce the anthesis of flower buds (Zacharias et al., 2008). To determine the duration from the flowering period to fruit ripening, average values of real evapotranspiration between 746 mm and 799 mm are needed (Nunes et al., 2010). Other models developed link the sequential analysis of images to the detection of flowering events, which are applied to predict the time to ripening of the fruits and the estimation of production (Peng et al., 2018).

Among the most prominent endogenous factors in coffee plant flowering are the expression patterns of the *SOC1* gene, which is involved in vernalization and autonomous pathways of flower induction. The *AGL2* gene, which is a mediator between the genes of the flower meristem and the identity of the flower organ, is expressed, and different expression patterns in floral and vegetative organs with the *AP3* orthologous *CaC09* and *CaC12* genes (De Oliveira et al., 2010). Considering the importance *NAC25* gene identified in *Coffea* species is expressed in floral tissues (Huded et al., 2022). In addition, 10 FRL homologs exhibit differential expression patterns during the development of flowers and fruits and

TABLE 4 Functions of phytohormones and environmental factors that trigger the phenological stages of flowering in coffee plants.

Phytohormone	Function	Environmental trigger	Phenological phase	References
Ethylene	Development of sexual organs, beginning of flowering	Decreased ethylene under water deficit conditions	Dormant flower buds,	Lima et al. (2021) and Alcantara-Cortes et al. (2019)
		Increased ethylene after rehydration	preanthesis and anthesis	
ABA	Growth inhibition, modulation of reproductive development	Increased ABA during the dry period	Dormant flower buds and	Mohan Ram and Rao (1984) and Lima et al. (2024)
		Decreased ABA levels following rehydration	preanthesis	
Gibberellins	Flowering induction	Increase in gibberellins after rehydration	Preanthesis	Browning (1973a)
Auxins (IAA; 2,4 D)	To direct and intervene in the processes of cell division, elongation, and differentiation	Increase in auxins after rehydration	Flower buds	Schuch et al. (1994) and Alcantara-Cortes et al. (2019)

TABLE 5 Summary of the key findings on the endogenous triggers of coffee flowering.

DOI (year) Ref	Country	Study type	Variables	Treatments	No. of repetitions	Sample size	Effects on flowering
Genes							
10.1007/s00344-024-11481-x (2024)[01]	Brazil	Inferential	Genes	2	4		The application of 1-MCP differentially modulates gene expression, decreasing the ethylene receptors *CaERS1-like*, *CaETR2-like*, *CaETR4-like* and *CaEIN4-like* and increasing the expression of *CaACO3-like* in flower buds.
10.1016/j.plaphy.2016.12.004 (2017)[09]	Brazil	Inferential	Genes	2	9		In flower buds, a high concentration of CAF is observed (263.75 mg/100 g fresh weight). Likewise, the genes *CaCYP76C4*, *CaCYP74A1* and *CaCYP82C2* involved in the biosynthesis of CAF and KAH, show greater activity in flowers.
10.1007/s00497-014-0242-2 (2014)[18]	Brazil	Inferential	Genes				The genes *CaAP1/CAL*, *CaAP3*, *CaPI* and *CaAG* are expressed at all stages of flowering. *CaAP1/CAL*, *CaAP3* and *CaTM6* are expressed initially in the inner bracts and the fundamental meristem and later in sepals and petals. *CaPI* and *CaAG* are expressed in vascular bundles, meristem, stamens and carpels.
10.1016/j.plgene.2023.100413 (2023)[22]	Brazil	Inferential	Genes			102	The *CaMADS7*, *CaMADS39*, *CaMADS35* and *CaMADS43* genes show specific expression in floral and meristematic tissues. *FLC* regulates the flower induction time.
10.1007/s12298-022-01235-y (2022)[29]	Brazil	Inferential	Genes	2	3	10	Under water deficit conditions, coffee plants express the genes *CaACS1*, *CaACS3* and *CaACO4* in flower buds and *CaACS3* in open flowers; in addition, the repression of the ACO genes and their roles as regulators leads to an increase of ACC during dry periods, which is decisive for anthesis.
Phytohormones							
10.1007/BF02902247 (1986)[13]	Cuba	Inferential	Phytohormones			6	The application of 200 ppm IAA delays the period of flower induction for 25 days, and the application of 100 ppm 2,4-D prolongs it for 20 days.
10.1007/BF00025279 (1990)[23]	Hawaii	Inferential	Phytohormones	2	5		The application of 100 $mg{\cdot}L^{-1}$ GA_3 in flower buds larger than 4 mm promotes early flowering (by 20 days).
10.1007/bf00386131 (1970)[24]	Kenya	Inferential	Phytohormones		4		ABA represents approximately 75% of the inhibitory activity present in the acidic ethyl acetate extract, which supports its direct involvement in the inhibition of flower development.
Secondary metabolites							
10.1016/j.plantsci.2024.112117 (2024)[38]	Belgium	Inferential	Secondary metabolites		3		In the floral structures of *C. arabica*, the highest concentration of theobromine is in the gynoecium (0.9 ± 0.2 mg/g). The caffeine concentration in flower buds is 8.6 ± 0.6 mg/g.

Units and acronyms in the table: 1-MCP = 1-methylcyclopropene, CAF = cafestol, KAH = kahweol, ACC = 1-aminocyclopropane-1-carboxylic acid, GA_3 = gibberellic acid, ABA = abscisic acid, IAA = indole-3-acetic acid.

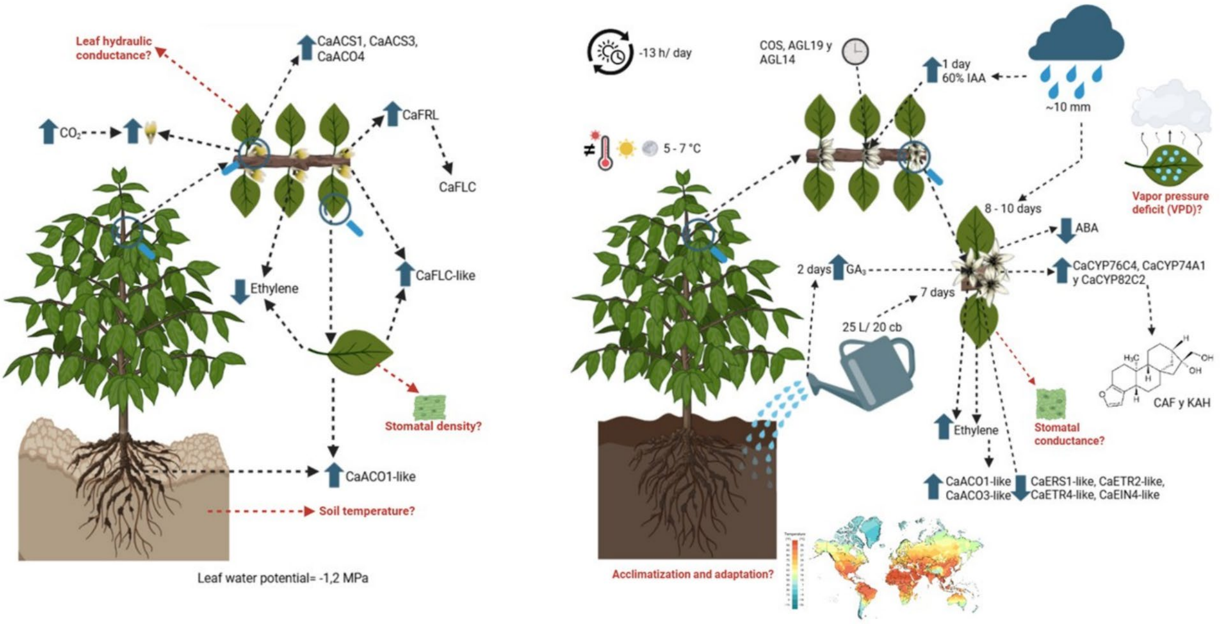

FIGURE 6
Response of coffee plants under two scenarios of water availability: water stress (left) and rehydration (right) during flowering. The relevant environmental and endogenous conditions during this phenological stage are shown. Ascending blue arrows (↑) indicate increases in gene expression and phytohormone concentration, whereas descending blue arrows (↓) indicate decreases in the same variables. The black dashed arrows indicate the factor and the plant organ to which it is related. The dashed arrows and question marks in red identify variables or conditions not identified in this review, indicating their potential relevance for future research on coffee flowering (Browning, 1973a; Mohan Ram and Rao, 1984; Schuch et al., 1994; DaMatta et al., 2007; Masarirambi et al., 2009; Barreto et al., 2012; Craparo et al., 2015; Boreux et al., 2016; Ivamoto et al., 2017; Vieira et al., 2019; Rakocevic et al., 2020; Lima et al., 2021; Santos et al., 2022; Rume et al., 2023; Unigarro et al., 2023; Lara-Estrada et al., 2024; Lima et al., 2024). Illustration created at https://BioRender.com.

regulate the expression of FLC, with a greater contribution of *CaFRL* genes in plants with pre-anthesis flower buds (Vieira et al., 2019).

Flowering in coffee plants involves different hormonal signaling pathways and gene interactions that are necessary to understand its molecular regulation (López et al., 2024). Ethylene responds to signaling after plant rehydration, at which point the content of 1-aminocyclopropane-1-carboxylate (ACC) increases significantly in all organs, especially in flower buds, where it increases 2.77-fold, through the transporter gene *LHT1* (López et al., 2022). This hormone is produced from the C3 and C4 carbons of methionine. Following this phase, S-adenosyl-L-methionine (AdoMet) is converted to 1-aminocyclopropane-1-carboxylic acid (ACC), then ACC is oxidized to form ACO, and finally ethylene is generated (Alonso and Ecker, 2001). In this context, the expression of these gene families has been studied in relation to the exogenous application of GA and ABA in *C. arabica*, with results indicating no changes in the expression of *CaACO3* during the induction and development of flower buds, and in the expression of *CaACS3* during induction. In contrast, there was an increase in *CaACS3* after the application of GA at 25 and 100 ppm during the development of flower buds, which could indicate an important response to the doses used during this phenological stage (Azevedo et al., 2025).

Consistently, signals following a rehydration event in coffee plants promote a decrease in ABA content and activate the onset of anthesis (López et al., 2022). In ABA biosynthesis, C40 β-carotenoids are the main precursors. The action of the enzyme 9-cis-cyclocarotenoid dioxygenase (NCED), responsible for catalyzing the breakdown of the C11 and C12 bonds of 9′-cis-violaxanthin and 9′-cis-neoxanthin, leads to the formation of xanthine (Mo et al., 2024). Regarding the enzymes involved in this pathway, the presence of three *CaNCED* genes and six *CaCYP707A* genes has been identified in *C. arabica*, which are essential for the oxidative degradation of ABA. In this regard, following the exogenous application of GA, an increase in the expression of the *CaNCED1* gene was observed during the induction and development of flower buds. In contrast, *CaCYP707A1* decreased with GA application during floral induction and showed no changes during flower bud development (Azevedo et al., 2025).

In addition to the role pivotal by ethylene and ABA in coffee flowering, there is evidence of the role of gibberellins. This phytohormone originates from geranylgeranyl diphosphate (GGPP), which is generated by isopentenyl diphosphate (IPP). Conversion to ent-kaureno results in GA12-aldehyde; which is finally converted into bioactive GAs, such as GA1 and GA4 (Salazar-Cerezo et al., 2018). Studies conducted on *C. arabica* report 16 *CaGA20ox* genes in the last step of the GA biosynthesis pathway, which catalyze the conversion of GA12 to GA9 and GA53 to GA20. Likewise, the exogenous application of GA and ABA did not modify the expression of *CaGA3ox1* during flowering induction, whilst the application of ABA increased the expression of this gene during flower bud development. The *CaGA2ox1* gene showed lower expression during induction and no changes during flower bud development (Azevedo et al., 2025).

Other key findings show that gibberellic acid (GA) activity increases in the number of flower buds, the number of flowers and the yield per plant (Schuch et al., 1990; Matsumoto and Lopez, 2016; Zapata and Guevara, 2020), In contrast, Zapata and Guevara (2020) find it is not clear the response to GA application during the main flowering periods.

Figure 6 presents the simplified main environmental conditions and endogenous factors that participate in the different stages of development of coffee flowering, as well as some important topics for future research. Short days of less than 13 h favor the initiation of flowering. Periods of water deficit, with potentials in the leaf of −1.2 MPa during the dormancy stage of the inflorescences, enable pre-anthesis after soil hydration (> 10 mm), together with fluctuations in daytime temperatures and night temperatures between 5 and 7 °C. Several genes involved in the flowering of coffee, namely, *CaFLC*, *CaERS* and *CaACO*, are determinants of the expression and responsiveness to both environmental stimuli and the hormonal activity of ethylene, ABA, IAA and GA_3. From the analysis of the studies reported in this manuscript, variables with potential for new investigations at the stomatal level in the leaf, such as soil temperature, air vapor pressure deficit, acclimatization and adaptation strategies, are identified.

5 Conclusion

The formulation of structured research questions and the development of a term matrix for the search strategy enabled the systematic identification of relationships between coffee flowering, environmental conditions, and the expression of specific genes and phytohormones across the developmental continuum from initiation to anthesis. Although pollinator-related studies were not part of the review's primary objective, their inclusion during the search process allowed the integration of complementary information relevant to the analyzed variables.

The extraction and synthesis of data following the PRISMA 2020 guidelines (Page et al., 2021), along with the validation and verification of findings, facilitated the identification of key variables grouped into categories encompassing hydric and thermal conditions, luminosity, gene families, and phytohormone types. Complementary studies retrieved outside the main search strategy enriched the analysis, underscoring the importance of consulting alternative sources to capture studies not indexed in conventional databases and to document potential search protocol limitations.

The analyzed studies consistently highlight that, beyond the activation of hormonal and genetic mechanisms, soil moisture represents one of the most critical determinants of coffee flowering. Adequate rehydration following a period of water deficit is essential to break floral bud dormancy and synchronize anthesis. These findings suggest that the strategic management of soil moisture constitutes a feasible agronomic approach to promote synchronized flowering and fruit ripening. However, the success of this strategy depends on local climatic conditions and production systems. In regions such as Brazil, where supplementary irrigation is available, rehydration timing can be optimized, whereas in rainfed systems, the onset and uniformity of flowering remain largely dependent on rainfall patterns.

Asynchronous flowering is associated with variations in gene expression, environmental conditions, and sugar metabolism. Genes expressed at specific levels in floral organs are linked to water stress responses and ethylene biosynthesis, and the identification of additional differentially expressed genes represents a valuable tool for breeding programs aiming to develop cultivars adapted to climate variability and capable of producing more uniform blooms.

Research on endogenous factors reveals a strong mechanistic link between plant water status and phytohormone dynamics: ethylene and gibberellin (GA_3) levels in buds increase following rehydration, whereas abscisic acid (ABA) levels decline over time. These findings point to the potential of exogenous application of phytohormones or hormonal inhibitors as strategies to induce more homogeneous flowering and reduce yield losses. Nevertheless, the effectiveness of such interventions depends on the developmental stage of nodes and buds, the inflorescence growth phase, and environmental conditions influencing physiological responses.

Future research should further investigate the factors triggering coffee flowering at the physiological and molecular levels, particularly focusing on stomatal dynamics, leaf and air vapor pressure deficits, and the role of climate change mitigation practices. Additionally, elucidating and validating the plant's physiological mechanisms under extreme climatic scenarios, while considering genotype-specific responses and agronomic management, will be crucial for improving the resilience and synchronization of coffee flowering in the face of global environmental change.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JR-S: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Writing – original draft, Writing – review & editing. CZ-M: Conceptualization, Validation, Writing – review & editing. JG-L: Conceptualization, Validation, Writing – review & editing. NC-A: Conceptualization, Validation, Writing – review & editing. MC-C: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. JV-L: Data curation, Formal analysis, Methodology, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2025.1711697/full#supplementary-material

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