Environmental Stress, Elicitors and Steviol Glycoside Production in Stevia rebaudiana: A Systematic Literature Review

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Abstract

Stevia rebaudiana is the primary natural source of steviol glycosides (SGs), compounds that provide intense sweetness without calories and have broad applications in food, pharmaceutical, and cosmetic industries. However, SG production is highly sensitive to environmental stresses and elicitor treatments, which modulate plant secondary metabolism. This systematic literature review aims to synthesize current research on how various environmental stresses and elicitors affect SG biosynthesis and yield in *S. rebaudiana*. Literature from databases including Scopus, Springer, ResearchGate, and Google Scholar was screened using the PRISMA framework, resulting in 74 eligible studies published between 2012 and 2024. The review reveals that abiotic stresses such as salinity, drought, light, chilling, and oxidative stress induce diverse responses depending on intensity and duration. Mild stress often enhances SG content, while severe stress reduces growth and total yield. Conversely, elicitors such as methyl jasmonate, salicylic acid, paclobutrazol, mannitol, and nanomaterials significantly promote stevioside and rebaudioside A accumulation by activating defense related metabolic pathways. Optimal elicitor concentrations (e.g., methyl jasmonate 60–120 μM, sodium silicate 25 mM, salicylic acid 0.5 mM) were identified to maximize metabolic enhancement. The findings highlight that integrating moderate stress with appropriate elicitor application can synergistically improve SG productivity. This review provides a comprehensive synthesis of mechanisms, trends, and knowledge gaps to support future research and industrial scale improvement of *S. rebaudiana* under stress and elicitation conditions.

1. Introduction

Stevia rebaudiana is widely known as the primary source of steviol glycosides, bioactive compounds that function as natural non-caloric sweeteners with a sweetness level 250–300 times greater than sucrose (Rybchuk et al., 2021). Steviol glycosides (mainly stevioside and rebaudioside A) have been declared safe by various global regulatory agencies, including the FDA (USA), EFSA (European Union), and JECFA, with “Generally Recognized As Safe” (GRAS) status and clear daily intake limits (Paucar *et al.*, 2023). Clinical and preclinical studies show that steviol glycosides are not toxic, mutagenic, carcinogenic, or cause serious side effects in humans at recommended doses (Ahmad et al., 2020). The demand for high-quality steviol glycosides in the food and pharmaceutical industries continues to increase, making research to improve the content of these compounds very important.

The production of steviol glycosides in Stevia rebaudiana is influenced by various environmental factors. Suboptimal environmental conditions such as drought, salinity, and extreme temperatures can trigger physiological and biochemical changes in plants (Ma et al., 2020), thereby affecting the biosynthetic pathway of steviol glycosides. Environmental stress can trigger changes in plant secondary metabolism depending on the type, intensity, and duration of stress. In some cases, mild stress such as moderate drought or low salinity can induce the accumulation of secondary metabolites as an adaptive response, thereby increasing the content of steviol glycosides (Purnowo et al., 2024).. Conversely, severe or prolonged stress can inhibit growth and reduce steviol glycoside production due to physiological and enzymatic disturbances, so that the effects of environmental stress on plant quality are not yet fully consistent and require a more comprehensive understanding (Hajihashemi *et al.*, 2016).

Therefore, in addition to environmental factors, the application of elicitors has been explored as another approach to enhance steviol glycoside accumulation in stevia. The use of elicitors as compounds that stimulate physiological responses or plant defenses has become an important strategy for increasing steviol glycoside production (Ghazal et al., 2024). Elicitors can be biotic or abiotic factors, such as methyl jasmonate, salicylic acid, or certain mineral compounds, showing positive effects on the accumulation of stevioside, rebaudioside A, as well as phenolic compounds and flavonoids (Rasouli *et al.*, 2021). The effect of the increase is highly dependent on the type, dose, and duration of application of the elicitor (Rahmawati et al., 2025). However, the effectiveness of elicitor types and concentrations varies between studies, requiring a systematic synthesis to understand consistent patterns and mechanisms.

There is a gap in the literature regarding the influence of environmental stress and elicitors on steviol glycoside production. Existing research results are scattered and sometimes contradictory, making it difficult for researchers and practitioners to draw clear conclusions. Therefore, this systematic literature review aims to summarize and analyze existing scientific evidence, identify research trends, methods used, and key findings, while providing recommendations for optimal strategies to increase the steviol glycoside content in Stevia rebaudiana.

2. Methodology

The publication and referenced in this analysis are derived from scholarly articles published in bibliographic database like Scopus and Springer, in addition to journal search engines such as Google Scholar and ResearchGate. The search keywords were “Stevia”, “Steviol glycoside”, and “Stress”. The authors examined literature pertaining to the subject of the systematic review, appraised the methodological rigor and dependability of the results, analyzed the outcomes reported in the chosen studies, and subsequently condensed and structured the data before incorporating the findings into a comprehensive systematic review.

2.1 Objective of the review

Systematic reviews have the following main review questions :

- What literature sources and data have been documented regarding the influence of stresses and elicitors on *Stevia rebaudiana*?

Additional questions used are :

- What types of stresses have been studied in relation to *Stevia rebaudiana?*
- What types of elicitors have been reported to affect steviol glycoside production?

- Which countries or regions have conducted studies on environmental stress and elicitor effects in *Stevia rebaudiana*?
- What are the emerging research trends and gaps in studies related to stress physiology and elicitation in *Stevia rebaudiana*?

2.1 The scope of the review

This systematic review concentrated on the aggregation, assestment, and integration of research findings regarding the effect of stress and elicitors on the production of steviol glycosides. A standardized ftamework approach, commonly utilized worldwide, was employed in this study to establish the revuew's parameters. Initially, the review identified the population, intervention, comparison, and outcome (PICO) to define the scope of the investigation (Methley et al., 2014; Shamseer et al., 2015; Fernández del Amo et al., 2018; Eyzaguirre and Fernandes, 2024). A more detailed explanation of the PICO framework used in this systematic review is :

- *Population* : *Stevia rebaudiana* Bertoni
- *Intervention* : Stress treatment or elicitor administration
- *Comparison* : Control plants without stress or elicitor
- *Outcome* : Changes in the levels and quality of steviol glycosides and the physiological responses of plants

2.3 Literature Search

The PICO approach was used prior to the literature search to obtain adequate and relevant literature coverage. This study solely concentrated on the PICO elements of population and intervention in order to broaden the scope of literature and prevent limiting the quantity of pertinent papers that could be located. Literature searches in ResearchGate, Springer, Google scholar and Scopus used English language (Table 1). In order to filter out less pertinent papers from the search outcomes, solely the initial 100 publications from every database and journal search engine were chosen.

Table 1
Literature search record

No	Database	Search string	Date of literature search	Search result
1	Research Gate	Stevia OR Steviol Glycoside AND Stress	04/08/2025	100
2	Springer	Stevia OR Steviol Glycoside AND Stress	04/08/2025	100
3	Google Scholar English	Stevia OR Steviol Glycoside AND Stress	04/08/2025	100
4	Scopus	Stevia OR Steviol Glycoside AND Stress	04/08/2025	100

2.4 Literature Screening

The significance of the research was established following the compilation of the literature review. The importance of the study was evaluated based on the inclusion criteria outlined in Table 2. The study must meet the requirements according to the previously identified PICO method, including the desired population intervention, comparison, and outcome to be included in the review. Initially, redundant search outcomes were excluded, followed by a two-phase screening procedure, with the initial phase involving evaluation of the title and abstract, and subsequent phase involving a through examination of the full-text content. All stages of questions formulated based on PICO to select studies that fit the scope of the review.

Table 2
Questions used to determine which studies to include and exclude during combined title and abstract and full-text screening.

Screening stages	Questions	Screening outcome
Title and abstract screening	• Does the study focus on stevia? • Does the study present assessment on steviol glycoside? • Does the study present stress abiotic or biotic stress? • Does the study present a relationship between stress and the levels of steviol glycoside in stevia?	Studies can be included if they answer all the questions
Full-text screening	• Do the steviol glycoside occur in stevia plant? • Does this study present data related to the percentage content of compounds such as stevioside, rebaudioside, etc? • Does the study mention the type of stress given to stevia? • Does the study present species of stevia? • Does this study provide an assestment of morphology, anatomy, physiology and biochemistry? Additional questions are included to obtain general information of the studies: • Publication type (J = journal article, P = Proceeding Conference, T = thesis, B = Book chapter, R = Review) • What is the type of the study? (F: field measurement, R: review, L: Laboratory, O: Opinion) • What is dataset presented in the study that relevant to review?	Studies are included if they satisfy at least two screening questions

2.4.1 Reporting and presentation

The results of this systematic review were reported and presented in accordance with the standardized reporting guidelines for systematic review of environmental studies (Mengist *et al.*, 2020).

2.4.2 Publication screening

The preferred reporting items for systematic reviews and meta analyses (PRISMA) serves as a framework for systematically conducted reviews, aiming to uphold transparararency and comprehensiveness in the review process, while also providing researchers with a structured approach to follow at each stage (Pati and Lorusso, 2018; Xiao and Watson, 2019; Dede et al., 2023). In initial stage, 400 publications were retrieved through a systematic literature search string, as presented in Table 1. Following the screening process of the literature based on the study's specific questions, a total of 74 pertinent papers were identified. This screening involved evaluating the title, abstract, and full-text of each paper.Only 18.5% of the initially identified studies (74 out of 400) met the inclusion criteria and were deemed eligible for data extraction and analysis. The findings of the literature searches conducted on the study databases revealed an estimation of the publications identified, including duplicate entries (Fig. 1).

The number of publications focusing on effect stress and elicitor in stevia from one in 2012 to six in 2015. The publication pattern from 2012 onwards exhibited a period of stagnation, characterized by one publication annually until 2014. Subsequently, there was no discernible trend, culminating in the highest number of publications in 2024, totaling 15 publications. Journal articles emerged as the predominant type of publication (Fig. 2)

3. Result

3.1 Distribution regarding research on the effects of stress and elicitors on stevia

The analysis revealed that research on steviol glycoside was conducted in various countries spanning twenty two different countries worldwide. A total of 74 research sites were identified and spread across twenty two countries, namely: Malaysia of Southeast Asia; China and Taiwan of East Asia; India and Pakistan of South Asia; Iran, Iraq, and Turkey of Western Asia (the Middle East); Morocco, Egypt, and Tunisia of North Africa; South Africa of Southern Africa; Russia and Romania of Eastern Europe; Poland of Central Europe; Italy of Southern Europe; Belgium of Western Europe; Brazil and Chile of South America; and the United States of North America.

Iran boasts the highest number of study sites, totaling 20, followed by India with 10 sites and China with 8. Other countries with multiple study sites include Pakistan (5), Turkey (3), Morocco (3), Belgium (3), Poland (3), and the United States (3). Additionally, Russia, Brazil, Malaysia, and Egypt each have 2 study sites. Notably, several countries are represented by only one study site, namely South Africa, Taiwan, Tunisia, Italy, Chile, Romania, and Iraq (Fig. 3).

3.2 Stress and Elicitor Impact on Steviol Glycoside Content

The effects of stress and elicitor application have been identified on the high and low content of steviol glycosides in Stevia rebaudiana, as shown in Table 3. The research samples were taken from stevia plants with control plants as a comparison. Salt stress is the most widely studied stress in terms of its effect on steviol glycoside content. Meanwhile, the most widely used elicitor in various types of stress is salicylic acid. The use of stress and various elicitors has been shown to significantly increase steviol glycoside (SGs) content, such as osmotic stress, gamma irradiation stress, oxidative stress, and water stress (Table 3). However, some studies have shown that stress reduces the content, such as salt stress, drought stress, short day length, light stress, and chilling stress.

The effects of stress are highly dependent on the type and concentration of stressors; excessively high concentrations can reduce growth and SG content (Pratibha et al., 2016). Elicitors such as silicon, mannitol, methyl jasmonate, paclobutrazol, steviol glycoside external, licorice extract, gamma rays, etc. can increase the production of stevioside and rebaudioside A, the two main components of SGs, but the application of humic acid actually reduces the steviol glycoside content. Stress on stevia can increase the content of SGs in plant tissues, but is often accompanied by a decrease in growth and biomass production (Wahyuni et al., 2025). Therefore, an elicitor is needed that can increase the expression of SGs biosynthesis genes, thereby accelerating and increasing the accumulation of stevioside and rebaudioside A (Cristina et al., 2019).

Table 3
The effect of stress and elicitors on steviol glycoside content of *Stevia rebaudiana* bertoni

Type of stress	Effects	Type of elicitor used	Effects	References
Salt stress	Decrease	Silicon (applied as foliar sodium silicate)	Increase	Yavaz *et al.*, 2019
Osmotic stress	Increase	Mannitol	Increase	Ghaheri *et al.*, 2019
Salt stress	Increase	Methyl jasmonate	Increase	Dhankot *et al.*, 2024
Salt stress	Decrease	Rhizospheric bacteria	Increase	Sun *et al.*, 2022
Drought stress	Decrease	Paclobutrazol	Increase	Karimi *et al.*, 2019
Drought stress	Decrease	Steviol glycoside external	Increase	Karimi *et al.*, 2015
Drought stress	Decrease	Licorice extract	Increase	Khshan *et al.*, 2024
Gamma irradiation stress	Increase	Gamma rays	Increase	Kumar *et al.*, 2024
Short day lenght	Decrease	Fluorescent warm white	Increase	Aziz *et al.*, 2021
Light stress	Decrease	Green light	Increase	Cheng *et al.*, 2025
Salt stress	Increase	Salicylic acid	Increase	Janah *et al.*, 2024
Salt stress	Increase	TiO_2 nanoparticles + Putrescine	Increase	Gerami *et al.*, 2024
Salt stress	Decrease	Melatonin	Increase	Vali *et al.*, 2021
Salt stress	Increase	Chitosan	Increase	Mahyar *et al.*, 2020
Chilling stress	Decrease	Salicylic acid	Increase	Sihem *et al.*, 2016
Oxidative stress	Increase	Hydrogen peroxide (H_2O_2)	Increase	Rabia *et al.*, 2017
Drought stress	Increase	Strigolactones	Increase	Ali *et al.*, 2025
Oxidative stress	Increase	Copper oxide nanoparticles	Increase	Rabia *et al.*, 2017
Water stress	Increase	Humic acid	Decrease	Khosarani *et al.*, 2023
Short day lenght	Decrease	Red LED light	Increase	Stijn *et al.*, 2012
Oxidatice stress	Increase	Polistiren Nanoplastic (PSNPs)	Increase	Coman *et al.*, 2023
Salt stress	Decrease	Glycine betaine	Increase	Abazar *et al.*, 2023
Drought stress	Decrease	Salicylic acid	Increase	Sahin *et al.*, 2023
Drought stress	Increase	Melatonin and TiO_2 NPs	Increase	Sheikhalipoir *et al.*,

Type of stress	Effects	Type of elicitor used	Effects	References
				2023
Salt stress	Increase	Endophytic fungi and exogeneous spermidine	Increase	Saravi *et al.*, 2022
Drought stress	Decrease	Humic acid	Decrease	Zamani et al., 2021

3.3 Elicitors and Optimal Concentrations in *Stevia rebaudiana*

Various elicitors have been reported to effectively enhance both the growth and steviol glycoside production. The data presented show that elicitors include a wide range of chemical, biological, and physical agents, each with specific optimal concentrations for achieving maximum metabolic response (while minimizing phytotoxicity) (Table 4). Chemical elicitors such as sodium silicate (25 mM), mannitol (20 g/L), methyl jasmonate (60–120 µM), salicylic acid (0.5 mM), and hydrogen peroxide (10 mM) have been shown to trigger defense related metabolic pathways, thereby stimulating secondary metabolite synthesis. Similarly, growth regulators such as paclobutrazol (12 ppm) and putrescine (1 mM) enhance plant biomass and modulate terpenoid biosynthesis, contributing to the increased accumulation of SGs.

Biotic and nano-based elicitors also exhibit significant effects on metabolic enhancement. Chitosan (0.4 g/L), licorice extract (6%), and chitosan-functionalized selenium nanoparticles (Cs-Se NPs, 20 mg/L) serve as potent biogenic elicitors that activate plant defense responses and improve the overall yield of SGs. The application of nanomaterials such as TiO_2 nanoparticles (10–300 ppm), silver nanoparticles (200 ppm), and multi-walled carbon nanotubes (50 mg) provides an additional stimulatory effect by improving reactive oxygen species (ROS) signaling and nutrient absorption efficiency, which ultimately favor secondary metabolite accumulation.

In addition, physical and light-based elicitors such as gamma rays (20 Gy), high light intensity (900 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and specific light spectra including green light (50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and fluorescent warm white light (100 W/m^2) have been reported to influence photosynthetic activity and carbon flux toward terpenoid biosynthesis. Novel elicitors such as nanocomposite Fe_3O_4/catechin (10 mg/L), strigolactones (0.01 mg/L), glycine betaine (50 mM), and melatonin (10 µM) represent emerging strategies to fine-tune stress signaling and secondary metabolism in stevia. Overall, the diversity of elicitors and their optimized concentrations demonstrate the complexity of regulatory mechanisms involved in SG biosynthesis, highlighting the potential of elicitor-based enhancement strategies for improving both yield and quality of steviol glycosides.

Table 4
Types and optimal concentration of elicitors used for enhancement of the growth and steviol glycoside of *Stevia rebaudiana* bertoni

Elicitors	Optimal Concentration	References
Sodium silicate	25 mM	Yavaz *et al.*, 2019
Mannitol	20 g/L	Ghaheri *et al.*, 2019
Methyl Jasmonate	60–120 μM	Dhankot *et al.*, 2024
Paclobutrazol	12 ppm	Karimi *et al.*, 2019
External steviol glycoside	200 ppm	Karimi *et al.*, 2015
Licorice extract	6%	Khshan *et al.*, 2024
Gamma rays	20 Gy	Kumar *et al.*, 2024
Fluorescent Warm White	100 Watts/m2	Aziz *et al.*, 2021
Green light	50 $\mu mol \cdot m^{-2} \cdot s^{-1}$.	Cheng *et al.*, 2025
Salicylic acid	0.5 mM	Janah *et al.*, 2024
TiO_2 nanoparticles	300 ppm	Gerami *et al.*, 2024
Putrecine	1 mM	Gerami *et al.*, 2024
Multi walled Carbon Nanotubes ($MWCNT_S$)	50 mg	Dariush *et al.*, 2022
Melatonin	10 μM	Vali *et al.*, 2021
Chitosan	0.4 g/L	Mahyar *et al.*, 2020
Hydrogen peroxide (H_2O_2)	10 mM	Rabia *et al.*, 2017
Strigolactones (SLs)	0.01 mg L^{-1}	Ali *et al.*, 2025
High light intensity	900 $\mu mol \cdot m^{-2} \cdot s^{-1}$	Karel *et al.*, 2022
Nanoplastik Polistiren (PSNPs)	10 mg/L PSNPs	Coman *et al.*, 2023
Glycine betaine	50 mM	Abazar *et al.*, 2023
Nanokomposit Fe3O4/Catechin	10 mg/L	Ghorbani *et al.*, 2025
TiO_2 NPs	10mg L^{-1}	Sheikhalipoir *et al.*, 2023
Spermidine	0.75 mM	Saravi *et al.*, 2022
Silver Nanoparticles (Ag NPs)	200 ppm	Abdull *et al.*, 2022

Elicitors	Optimal Concentration	References
Chitosan-Functionalized Selenium Nanoparticles (Cs-Se NPs)	20 mg L^{-1}	Sheikhalipoir *et al.*, 2021

3.4 Abiotic Stress and Steviol Glycoside Biosynthesis

Abiotic stress on stevia can increase the steviol glycoside content per dry weight, but generally reduces growth and leaf production. For optimal production, a balance between stress levels and plant growth is required. Mild to moderate stress, such as treatment with polyethylene glycol (PEG) or salt (NaCl), can increase the content of SGs (stevioside, rebaudioside A) by several times compared to controls. This occurs because stress triggers a plant defense response that increases the production of secondary metabolites, including SGs (Khan et al., 2024). Most studies show that abiotic stress causes a decrease in growth, such as the number of leaves, shoot length, dry weight, and number of roots. At high stress concentrations, plant growth decreases dramatically, even though the SG content per gram of tissue increases (Magangana et al., 2021). Although the SG content per dry weight increases, the total SG yield per plant or per hectare may decrease because the total biomass produced is lower (Zamani et al., 2021). Therefore, excessive stress is not recommended for large-scale production.

The biosynthetic pathway of steviol glycosides (SGs) in Stevia rebaudiana under abiotic stress occurs through three main subcellular stages: it begins in the plastids via the MEP pathway within the plastids. At this stage, precursor compounds such as isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP) are produced as the building blocks for terpenoid formation. These two precursors then play an important role in the formation of ent-kaurene, which is the initial compound that forms the basis for steviol synthesis. Next, the ent-kaurene formed in the plastids is transferred to the endoplasmic reticulum (ER) membrane to undergo oxidation and cyclization. Inside the ER, a series of biochemical reactions convert ent-kaurene into ent-kaurenoic acid, then into steviol. This stage is a key process that links the formation of precursors in the plastids with the final stage of glycoside formation (Fig. 4). The final stage takes place in the cytosol, where the steviol compound undergoes glycosylation, which is the addition of sugar groups through enzymatic reactions. This process produces various types of steviol glycosides, such as stevioside and rebaudioside, which determine the sweetness level of stevia leaves.

4. Conclusions

This systematic literature review highlights the significant influence of environmental stress and elicitor application on the biosynthesis and accumulation of steviol glycosides (SGs) in *Stevia rebaudiana*. The synthesis of data from 74 publications indicates that stress factors particularly salinity, drought, light intensity, and temperature variation play dual roles, either enhancing or suppressing SG content depending on stress type, concentration, and exposure duration. Mild to moderate abiotic stress can stimulate secondary metabolism and upregulate genes involved in terpenoid biosynthesis, resulting in elevated stevioside and rebaudioside A levels. In contrast, severe or prolonged stress reduces growth and overall SG yield due to impaired physiological and enzymatic processes. Elicitors, both biotic and abiotic, have proven effective in optimizing SG production through metabolic reprogramming. Compounds such as methyl jasmonate, salicylic acid, mannitol, and nanomaterial-based elicitors significantly enhance plant defense responses and secondary metabolite accumulation when applied at optimal concentrations. Moreover, the integration of nanotechnology and controlled light treatments offers promising strategies for improving plant productivity and metabolite quality. Overall, combining moderate stress with appropriate elicitor treatments provides a synergistic approach to enhancing SG yield while maintaining plant health. Future research should focus on molecular-level elucidation of SG biosynthetic regulation, identification of stress and elicitor interaction pathways, and the development of scalable cultivation systems. These findings contribute to advancing sustainable production strategies for *Stevia rebaudiana* as a high value natural sweetener crop.

Declarations

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Authors’ Contributions

Riska Wahyuni designed the research concept, conducted the literature search, data extraction, and analysis, and drafted the initial manuscript. Nida Wafiqah Nabilah M. Solin contributed to the supervision, conceptual guidance, and critical revision of the manuscript. Chairani Hanum assisted in data analysis and interpretation. Lisa Mawarni contributed to literature review and manuscript editing. Tiara Septirosya assisted in data collection and final manuscript preparation. All authors read and approved the final version of the manuscript.

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Data Availability

No datasets were generated or analysed during the current study

Clinical Trial

Not applicable

Ethics approval and consent to participate

Not applicable. This review article is entirely based on previously published research and does not involve any new data from human or animal subjects; hence, ethical approval was not necessary.

Consent for publication

Not applicable

Competing interest

The authors declare that there no conflict of interest regarding the publication of this manuscript. In addition, the ethical issues, including plagiarism, informed consent, misconduct, data fabrication or falsification, double publication or submission, and redundancy, were observed by the authors.

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Figures

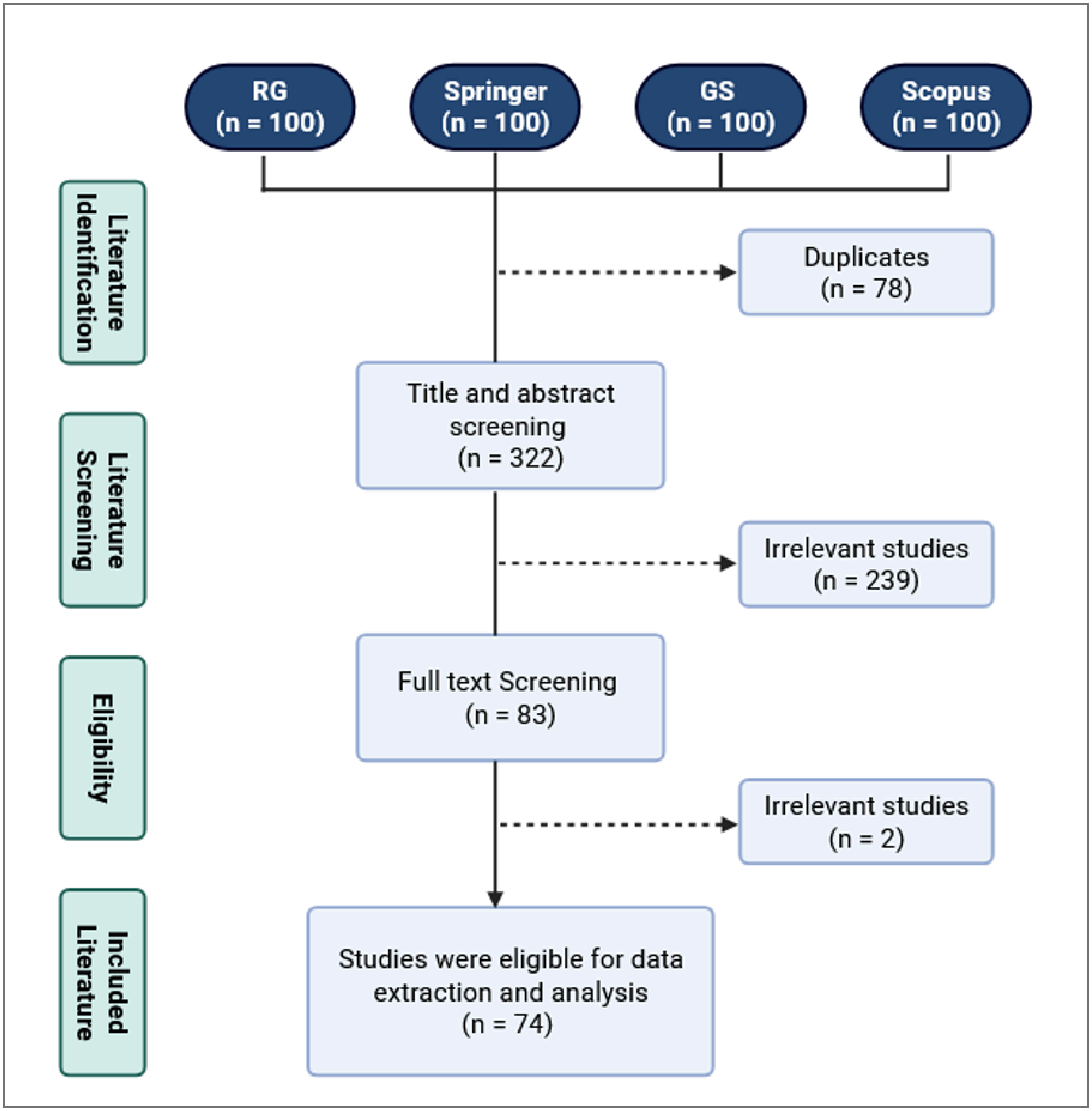

Figure 1

The prisma flow diagram illustrates the process of selecting eligible studies

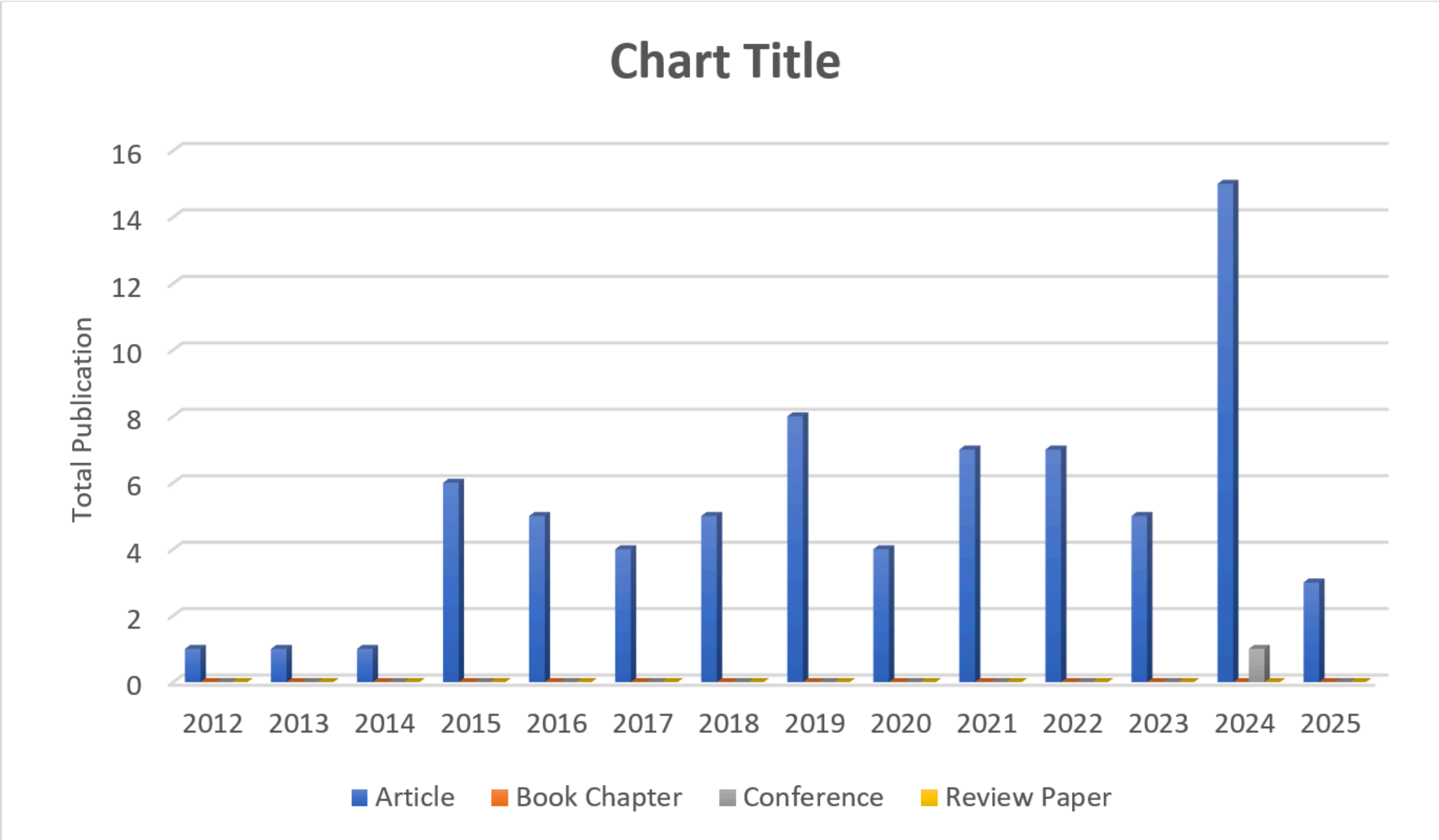

Figure 2

The trend of publication on steviol glycoside in stevia (year vs the number of publication and types of publication

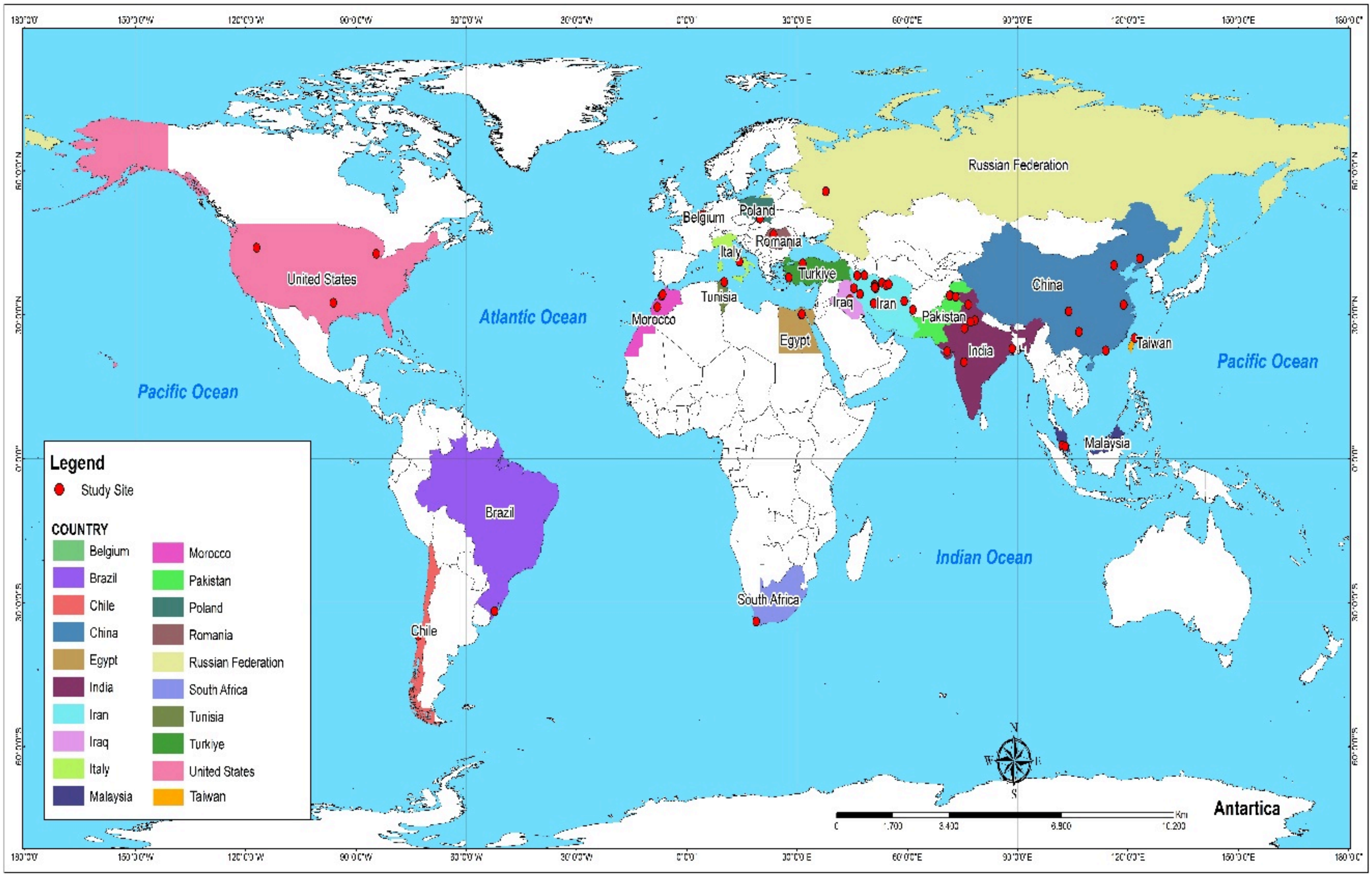

Figure 3

Geographical distribution of studies on steviol glycoside impact of stress reported between 2012-2025. The data were compiled through systematic review

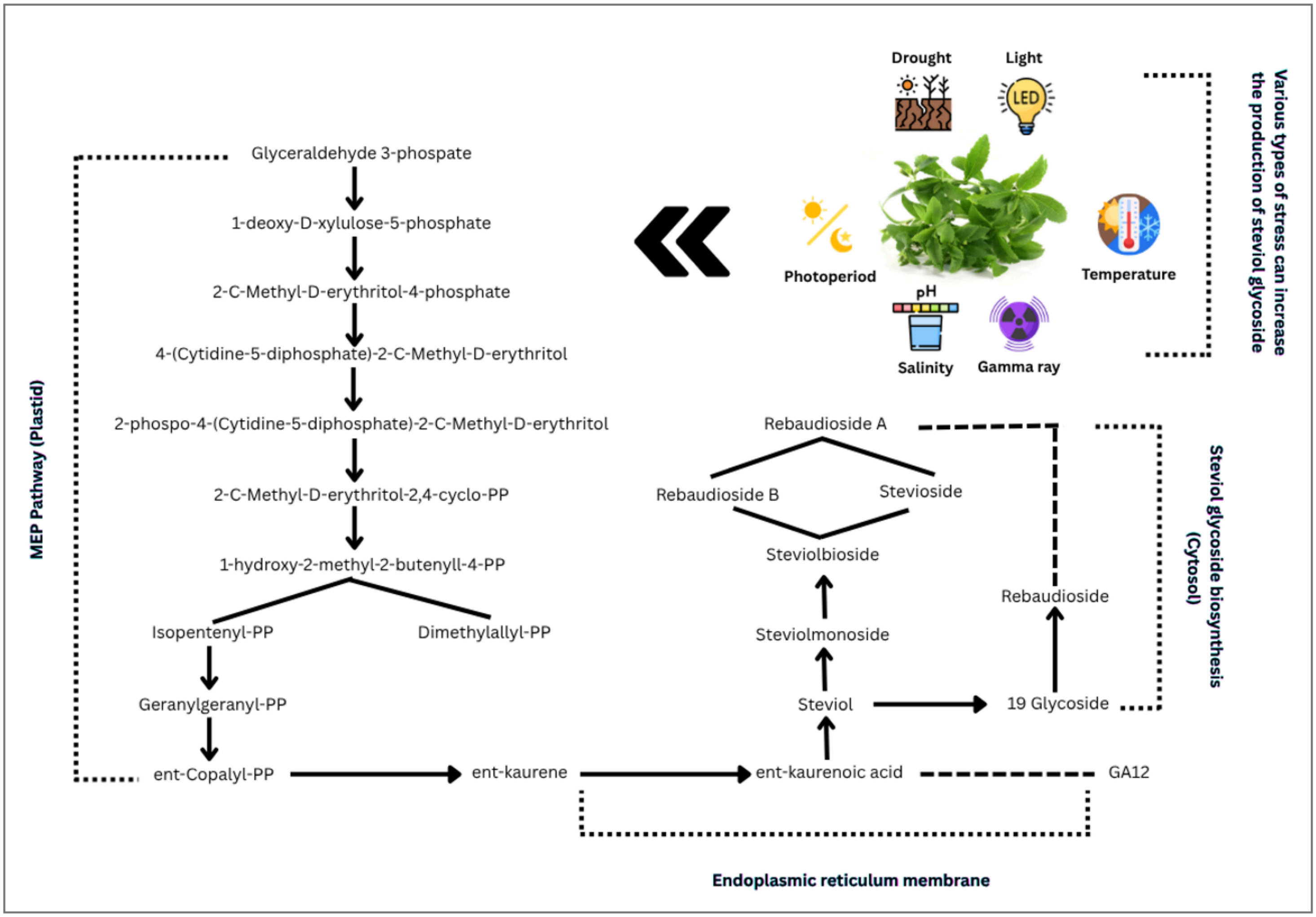

Figure 4

Various types of stress can icrease the production of steviol glycoside (SGs) and biosynthesis pathway under abiotic stress