Analysis of Histochemical Localization and Content Influencing Factors of Saponins in *Pseudostellaria heterophylla*

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Abstract This paper provides a systematic review of the histochemical localization, content characteristics, and influencing factors of saponins in *Pseudostellaria heterophylla* based on an extensive literature survey. It provides an in-depth analysis and summary of the effects of biological factors, environmental conditions, agronomic practices, processing methods, and continuous cropping obstacles on the synthesis of *P. heterophylla* saponins, as well as their underlying mechanisms. Based on identified gaps in the current literature, future research directions and prospects are proposed. The findings of this review offer valuable insights for advancing the understanding of the saponin biosynthesis mechanisms in *P. heterophylla* and for enhancing its quality.

Key words *Pseudostellaria heterophylla*, Saponin, Histochemical localization, Content influencing factors, Research progress

1 Introduction

Pseudostellaria heterophylla refers to the dried tuber of *P. heterophylla* (Miq.) Pax ex Pax et Hoffm, a species belonging to the Caryophyllaceae family[1]. It is primarily cultivated in regions such as Fujian, Guizhou, and Hebei. This plant was first documented in the *New Compilation of Materia Medica* during the Qing Dynasty[2]. *P. heterophylla* contains a variety of bioactive compounds, including polysaccharides, saponins, cyclic peptides, and volatile substances[1,3], and exhibits both medicinal and nutritional properties. It is characterized by a mild nature and is traditionally believed to promote the production of body fluids, moisten the lungs, benefit qi, strengthen the spleen[4], maintain health, and enhance immune function. Furthermore, Zherong *P. heterophylla* has been designated as part of the 2025 Agricultural Brand Quality Cultivation Plans by the Ministry of Agriculture and Rural Affairs of the People's Republic of China. *P. heterophylla* saponins primarily consist of triterpenoids and are significant secondary metabolites as well as active medicinal components of the plant. Research has demonstrated that triterpenoids possess notable antioxidant properties and exhibit diverse pharmacological effects, including immune protection and regulation of intestinal function[5]. Furthermore, with respect to pharmaceuticals, the National Medical Products Administration mandates that the content of *P. heterophylla* saponins in *P. heterophylla* formula granules should range from 6.0 to 21.0 mg/g. As a significant group of active compounds in *P. heterophylla*, saponins have not been systematically reviewed or synthesized in the existing literature concerning their histochemical localization and the factors influencing their content. To date, comprehensive studies on *P. heterophylla* saponins remain unavailable. This paper presents a comprehensive review of the histochemical localization, content, and influencing factors of saponins in *P. heterophylla*, based on an extensive literature survey and synthesis. It systematically analyzes the effects and underlying mechanisms of biological factors, environmental conditions, agronomic practices, processing methods, and continuous cropping obstacles on the biosynthesis of *P. heterophylla* saponins. Furthermore, the study offers recommendations and future research directions to support advanced investigations into the synthesis of these saponins and the enhancement of *P. heterophylla* quality.

2 Histochemical localization and content characteristics of saponins in *P. heterophylla*

P. heterophylla is a traditional Chinese medicinal plant that is cultivated during the winter and harvested in the summer. The medicinally valuable part of the plant is its tuberous root, while its fibrous roots have also been utilized in the development of novel veterinary pharmaceuticals. The tuberous roots of cultivated *P. heterophylla* originate from adventitious roots. Following winter planting, the tuberous roots sprout, and the plant produces leaves and flowers from February to middle March of the subsequent year. Between April and May, the plants exhibit vigorous growth, during which the adventitious roots develop into tuberous roots. From late June to July, the stems and leaves begin to wither, signaling the appropriate time for harvesting the tubers. *P. heterophylla* saponins are primarily triterpenoid compounds. Their biosynthesis and accumulation are governed by complex factors, including genetic determinants and environmental conditions. These saponins are synthesized and distributed throughout the stems, leaves, tubers, and fibrous roots of *P. heterophylla* (Fig. 1A). A statistical analysis of the existing literature[6-8] indicates that the average

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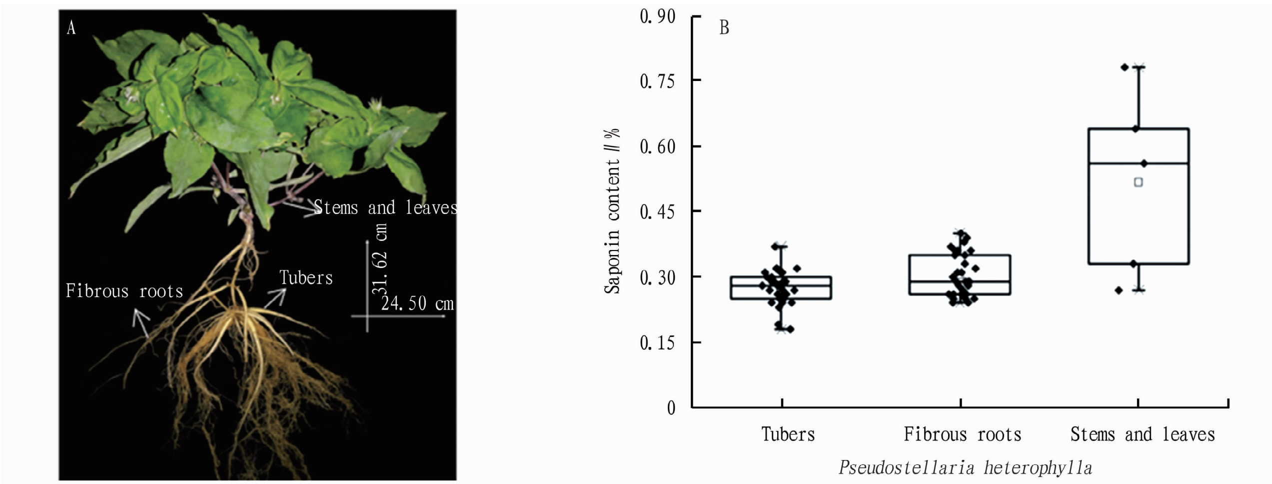
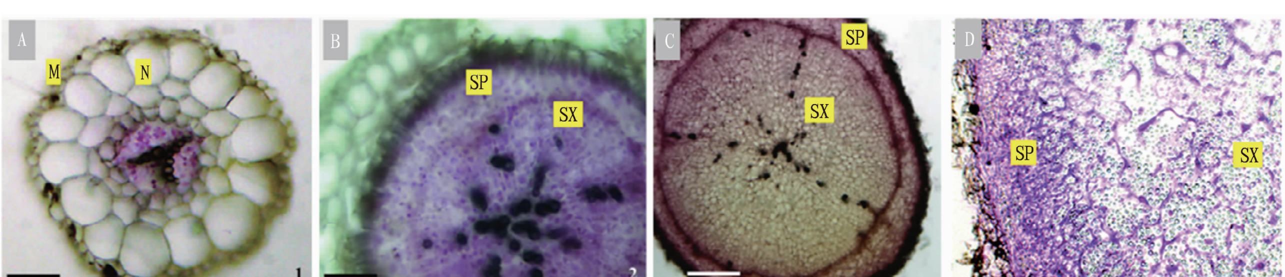
concentrations of saponins in the tubers, fibrous roots, and stems and leaves of *P. heterophylla* are 0.27%, 0.31%, and 0.51%, respectively (Fig. 1B). Notably, the saponin content exhibits a distribution pattern whereby the concentration in the stems and leaves exceeds that in the fibrous roots, which in turn is higher than that in the tubers. Specifically, the saponin content in the fibrous roots is approximately 1.15 times greater than that in the tubers. Furthermore, within dried *P. heterophylla* tubers, saponin contents are elevated at both the proximal (head) and distal (tail) ends of the root compared to the central region[9].



NOTE A. The *P. heterophylla* plant was collected in April; B. The data were obtained from references[6-8].

Fig. 1 Plants and saponin content of *Pseudostellaria heterophylla*

The synthesis and accumulation of saponins in *P. heterophylla* occur throughout its entire developmental and growth processes. The adventitious roots of the tuberous roots at various developmental stages sequentially progress through the promeristem, primary meristem, primary structure, and secondary structure phases. Upon entering secondary growth, the vascular cambium of the adventitious roots actively produces substantial amounts of secondary xylem inwardly and secondary phloem outwardly, resulting in the formation of swollen, spindle-shaped tuberous roots[9]. The reaction of vanillin mixed reagent with triterpene saponins produces a color change from light red to red and subsequently to purplish red, with the intensity of the color being directly proportional to the saponin content. Histochemical localization of the color development indicates the presence of saponin components within the parenchyma cells of the pericycle and the primary phloem in the primary structure of the adventitious roots of *P. heterophylla* (Fig. 2A). The parenchyma cells of the secondary phloem and secondary xylem in the secondary structure of adventitious roots contain saponin components (Fig. 2B). In the tuberous structures at the swelling and mature stages, parenchyma cells within the secondary phloem—excluding sieve tubes and companion cells—and parenchyma cells within the secondary xylem—excluding vessel elements—also contain saponin components (Fig. 2C). In mature microtuberous roots, saponins are predominantly localized in the vascular parenchyma cells of both the secondary xylem and phloem, with a higher content observed in the secondary phloem compared to the secondary xylem (Fig. 2D). In summary, within the primary structure of the root of *P. heterophylla*, saponins are localized in the parenchyma cells of the pericycle and the primary phloem. In the secondary structures and mature tubers, saponins are distributed throughout various cells of the periderm and secondary vascular tissues, excluding the cork layer and vessels. Notably, the highest content of saponins is observed in the secondary phloem.



NOTE A, B, and C were obtained from reference[9], and D was sourced from reference[10]. M. Epidermis; N. Cortex; SP. Secondary phloem; SX. Secondary xylem.

Fig. 2 Histochemical localization of saponins in *Pseudostellaria heterophylla*

3 Influencing factors of saponin synthesis and accumulation in *P. heterophylla*

3.1 Biological factors Genetic factors of *P. heterophylla* germplasm play a crucial role in the synthesis and variation of saponin content within this species. Ma Yang *et al.*[11] demonstrated significant differences in saponin content among varieties of *P. heterophylla* originating from Zherong, Fujian (ZS1, ZS2); Jurong, Jiangsu (JR); Shibing, Guizhou (SB); and Xuancheng, Anhui (XC). Notably, the highest saponin content was observed in the Zherong, Fujian varieties (ZS2), followed by those from Jurong, Jiangsu, and Shibing, Guizhou. The saponin content in the varieties from Xuancheng, Anhui (XS), and Zherong, Fujian (ZS1) was comparatively lower. Furthermore, Xu Rong *et al.*[12] reported no significant differences in saponin content among seedlings of the same variety but different grades, suggesting that genetic factors inherent to *P. heterophylla* germplasm significantly influence the synthesis and accumulation of saponins in this species.

3.2 Environmental factors

3.2.1 Light. Light plays a crucial role in the growth, development, and primary metabolism of *P. heterophylla*. Additionally, light intensity, duration, and quality influence the synthesis and accumulation of saponins in *P. heterophylla*. Wang Hanqi[13] reported that intercropping combined with shading significantly increased the saponin content in the tubers of *P. heterophylla*. Specifically, compared to the conventional planting control group, shading resulted in a 2.46-fold increase in saponin content. Wang Yan *et al.*[14] reported that optimal growth of *P. heterophylla* was achieved under 30% shading treatment. Shading significantly decreased enzyme activity and malondialdehyde content in the leaves of *P. heterophylla*, whereas excessive light intensity potentially caused leaf damage, leading to a reduction in saponin content. Similarly, Tian Xin *et al.*[15] found that 44% shading treatment significantly increased the relative abundance of beneficial soil microorganisms, such as basidiomycetes, thereby enhancing soil fertility, reducing disease risk, and promoting the growth and development of *P. heterophylla*. In summary, providing shade during the cultivation of *P. heterophylla* and moderately reducing light intensity are advantageous for its growth and the biosynthesis of saponins.

The duration of light exposure is a critical factor influencing the synthesis and accumulation of saponins in *P. heterophylla*. The duration of light exposure and changes in light intensity affect the growth and substance metabolism of *P. heterophylla* plants. Yang Furong *et al.*[16] reported a highly significant positive correlation between the average annual sunshine duration and the saponin content in *P. heterophylla*. Under specific conditions, extended sunshine duration promotes the accumulation of saponins in *P. heterophylla*. These findings suggest that, under appropriate light intensity, prolonging the annual sunshine duration positively contributes to the synthesis and accumulation of saponins in *P. heterophylla*.

Light quality, defined by the wavelength composition of light, constitutes a critical environmental factor influencing the growth and development of medicinal plants. Various light qualities exert distinct effects on plant morphology, metabolism, and physiological characteristics. Huang Yanfen *et al.*[17] demonstrated that different light qualities significantly impact the content of functional components and yield of *P. heterophylla*, with red light notably enhancing the saponin content. Consequently, it is plausible to hypothesize that the synthesis of saponins in *P. heterophylla* is associated with the extent to which red light induces the expression of key enzyme genes involved in its biosynthetic pathway.

3.2.2 Temperature. Temperature is a critical environmental factor influencing the growth of *P. heterophylla* and plays a vital role in the physiological and metabolic processes underlying its development. Yang Furong *et al.*[16] investigated the effects of seasonal factors on the saponin content of *P. heterophylla* and found that low temperatures during the coldest quarter promoted saponin formation, while higher temperatures in the hottest season enhanced saponin accumulation. Furthermore, the saponin content exhibited a dynamic pattern characterized by an initial negative correlation, followed by a positive correlation, and then a negative correlation with average monthly temperature. Regions exhibiting minimal temperature fluctuations were favorable for saponin accumulation, corroborating the findings of Kang Chuanzhi *et al.*[18], who identified the average temperature during the warmest season and thermal stability as the most significant environmental factors influencing the cultivation and distribution of *P. heterophylla*.

3.2.3 Moisture. Moisture is an essential factor for the growth and development of *P. heterophylla*. Under natural conditions, this species is susceptible to environmental stresses such as drought and waterlogging, which significantly affect the biosynthesis and accumulation of its saponins. Ma Yang *et al.*[19] reported a significant negative correlation between *P. heterophylla* saponin content and monthly precipitation. Similarly, Wei Dequn[20] found that drought stress during the plant's growth period significantly increased saponin content, whereas water retention stress led to a decrease. It is hypothesized that drought-related compounds in *P. heterophylla*, such as monoterpenoids, may be converted into triterpenoids and other compounds, thereby contributing to the plant's protective mechanisms under drought conditions. Furthermore, Yang Furong *et al.*[16] observed a negative correlation between saponin content and both average annual precipitation and relative humidity, suggesting that lower water availability is associated with higher saponin accumulation. These findings indicate that environments characterized by reduced rainfall and low humidity may be more conducive to the synthesis and accumulation of *P. heterophylla* saponins.

3.2.4 Altitude. Altitude variations often directly influence temperature, light intensity, and ultraviolet radiation levels, thereby affecting the synthesis and accumulation of saponins in *P. heterophylla* either directly or indirectly. Liu Bangyan *et al.*[21] reported that *P. heterophylla* cultivated at a high altitude of 2 157 m, compared to a conventional altitude of 677 m, exhibited increased yield and saponin content, but high-altitude cultivation was not favorable for the accumulation of polysaccharides in *P. heterophylla*. Similarly, Jiang Yuanbin[22] observed that *P. heterophylla* grown at 927 m, as opposed to 538 m, showed elevated saponin content in samples harvested during June, July, and August, with the highest saponin concentration recorded in July at 927 m. These findings suggest that higher altitudes may promote the synthesis and accumulation of saponins in *P. heterophylla* to some extent.

3.3 Agronomic methods Agronomy plays a crucial role in all aspects of the cultivation of *P. heterophylla*, significantly influencing its growth, development, and material metabolism. Li Bo *et al.*[23] reported that crop rotation methods for *P. heterophylla* enhanced the content of saponins and polysaccharides and its yield compared to intercropping, successive cropping, and continuous cropping. Notably, the saponin content in *P. heterophylla* reached up to 0.29% under rotation. Wu Yuxiang *et al.*[24] found that the application rates of nitrogen and potassium fertilizers were highly significantly correlated with the saponin content, while phosphorus fertilizer application also showed a significant correlation. The highest saponin content, reaching 0.49%, was observed at fertilizer application rates of nitrogen at 155 kg/ha, phosphorus at 140 kg/ha, and potassium at 90 kg/ha. Ma Zhiqiang *et al.*[25] reported that formula fertilization—comprising nitrogen (105 kg/ha), phosphorus (90 kg/ha), potassium (90 kg/ha), and organic fertilizer (1500 kg/ha)—significantly increased the saponin content of *P. heterophylla*, reaching 0.28%. Zhang Meng *et al.*[26] found that the application of the growth regulator gibberellin (GA) at a concentration of 20 mg/L resulted in the highest saponin content in *P. heterophylla*, which was 0.22% greater than that observed in the untreated control group. The effect of GA on saponin content exhibited a concentration-dependent response, promoting saponin accumulation at low concentrations and inhibiting it at high concentrations. Additionally, the application of indolebutyric acid (IBA) and kinetin (KT) was found to reduce the saponin content in *P. heterophylla*. Zhang Chen *et al.*[27] reported that the application of GA increased the saponin content in *P. heterophylla*, whereas abscisic acid (ABA) decreased it. GA may promote saponin accumulation by influencing methyl jasmonate (MeJA), while ABA may reduce saponin content by inhibiting the expression of key enzyme genes involved in saponin biosynthesis.

3.4 Processing methods Following the harvest of *P. heterophylla*, prompt processing is essential, primarily involving cleaning, drying, and screening. Among these steps, the drying process notably influences the saponin content of *P. heterophylla*. Wu Yuxiang *et al.*[28] reported that air-dried *P. heterophylla* exhibited the highest saponin content (0.51%), which was 1.94 times greater than that of blanched *P. heterophylla*. Therefore, washing the harvested *P. heterophylla* and air-drying it in a cool, well-ventilated environment is beneficial for enhancing its saponin content. Xu Rong *et al.*[29] reported that air-drying following steaming, hot air drying at 60 ℃ after steaming, and microwave vacuum drying of *P. heterophylla* resulted in higher saponin content compared to other processing methods. Wu Zengguang *et al.*[30] found that the saponin content of *P. heterophylla* was the highest (0.32%) when thoroughly boiled with 8 times the volume of water and subsequently dried at 60 ℃, whereas air-drying led to a decrease in saponin content (0.18%). Although this finding differs somewhat from the report by Wu Yuxiang *et al.*, it aligns with the steaming results reported by Wu Zengguang *et al.* Additionally, Zeng Lina *et al.*[31] demonstrated that drying temperature significantly influenced the saponin content of *P. heterophylla*, with saponin content ranking as follows: drying at 80 ℃ > natural sun-drying > drying at 60 ℃.

3.5 Continuous cropping obstacles *P. heterophylla* is a medicinal plant susceptible to continuous cropping obstacles, which adversely impact its yield, the concentration of active components, and the composition of soil microbial communities[32-33]. Wu Yuxiang *et al.*[24] reported that, compared to the control group, the saponin content in *P. heterophylla* subjected to continuous cropping obstacles decreased significantly by 18.75%. Similarly, Zeng Lingjie *et al.*[34] found that the saponin content in the continuous cropping obstacle group was 44.33% of that observed in the rotational cropping group. Furthermore, continuous cropping was associated with photosynthetic dysfunction and a reduction in the photosynthetic rate of *P. heterophylla*. Li Bo *et al.*[23] and Zhao Kai *et al.*[35] reported that after more than three years of continuous cultivation of *P. heterophylla*, the saponin content was significantly lower compared to the control group. It is feasible to cultivate *P. heterophylla* for consecutive 2 years in production, but extending the continuous cropping period results in a decline in quality indicators, including saponin content. This decline may be attributed to continuous cropping obstacles that reduce the photosynthetic rate of *P. heterophylla*, thereby hindering the effective accumulation and transformation of energy and saponin precursor organic matter, ultimately leading to decreased saponin content.

4 Prospects

The tubers of *P. heterophylla* develop through the expansion of adventitious roots. The biosynthesis of saponins in *P. heterophylla* occurs throughout the plant's entire growth and developmental stages. The primary constituents of these saponins are triterpenoids, which exhibit antioxidant properties as well as immune-enhancing and immune-restorative activities. The synthesis and accumulation of these compounds are intricately regulated by a combination of genetic factors and environmental conditions. Through a literature review, this study systematically analyzed and summarized the histochemical localization, content characteristics, and influencing factors of *P. heterophylla* saponins. It primarily focused on examining the effects of biological factors, environmental conditions, agronomic practices, processing methods, and continuous cropping obstacles on the synthesis of *P. heterophylla* saponins, as well as the underlying mechanisms involved. Studies have demonstrated that saponins derived from *P. heterophylla* are extensively distributed throughout the stems, leaves, tubers, and fibrous roots of the plant. Notably, the saponin content is higher at both the proximal and distal ends of the dried tuber compared to the central region. Histochemical localization analyses revealed that saponins are present in various cells of the periderm and secondary vascular tissues, excluding the cork layer and vessels within the secondary structure and mature tuberous roots. Among these tissues, the secondary phloem exhibits the highest saponin content.

The genetic characteristics of *P. heterophylla* germplasm are the primary biological factors underlying variations in saponin synthesis and content. Environmental factors such as light intensity, temperature, moisture, and altitude serve as critical influences. Specifically, moderate reductions in light intensity, prolonged annual sunshine duration, and exposure to red light irradiation have been shown to enhance the saponin content in *P. heterophylla*. Furthermore, agronomic practices, including crop rotation, balanced fertilization, and the application of growth regulators, alongside post-harvest drying methods, significantly impact saponin content. Additionally, continuous cropping obstacles may directly or indirectly contribute to a decline in the saponin content of *P. heterophylla*.

Currently, research on *P. heterophylla* saponins remains insufficient in several areas. The interdisciplinary integration of modern biotechnology, artificial intelligence, and related fields is expected to provide substantial support for both fundamental research and the translational application of *P. heterophylla* saponins. To expedite the application and practical implementation of these studies, it is recommended that future research focus intensively on the following three aspects.

(i) A multi-factor interaction analysis should be conducted to identify the primary active factors influencing the synthesis of saponins in *P. heterophylla* and to elucidate their interaction mechanisms. Furthermore, a comprehensive analysis of the systematic network comprising biological and abiotic factors regulating saponin synthesis should be performed to enhance saponin content in *P. heterophylla* through targeted strategies, including the development of new varieties, optimization of cultivation techniques, and assessment of regional suitability.

(ii) By employing multi-omics technologies in conjunction with large-scale computational data analysis, the biosynthetic metabolic pathway of *P. heterophylla* saponins can be comprehensively elucidated. This approach facilitates the identification of functional genes involved in the synthetic pathway and enhances the construction and characterization of key enzyme gene libraries. Utilizing functional genomics tools such as CRISPR-Cas9, a mutant gene library related to saponin biosynthesis in *P. heterophylla*, along with a mediated transformation system, has been developed to clarify the critical regulatory steps within the saponin synthesis pathway. Concurrently, the physicochemical properties of saponins in the plant's high-synthesis tissues, as well as associated transport proteins and their mechanisms, are thoroughly investigated.

(iii) The biotransformation and large-scale production of *P. heterophylla* saponins are accomplished through techniques including *in vitro* cell culture, tissue culture, and suspension culture of fibrous roots. By investigating exogenous interventions, such as the application of compound plant hormones or growth regulators, the natural synthesis of saponins during plant growth and development can be modulated to enhance saponin yield in *P. heterophylla*.

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