

## Comparative Study on Pistil and Stamen Development in Pin-type and Thrum-type Flowers of Tartary Buckwheat (Postprint)

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### Abstract

To elucidate the morphological differences in the development of the two floral morphs of common buckwheat (*Fagopyrum esculentum*), this study employed paraffin sectioning to observe and compare megasporogenesis, microsporogenesis, and the development of female and male gametophytes in pin and thrum flowers. The results demonstrated high similarity in cytological characteristics of pistil and stamen development between the two floral morphs, including orthotropous ovules, bitegmic integuments, and crassinucellate nucelli; megaspore tetrads arranged linearly with the functional megaspore at the chalazal end, and Polygonum-type embryo sacs. The anthers were tetrasporangiate, with the pollen sac wall comprising epidermis, endothecium, a single middle layer, and a single tapetal layer, wherein the tapetum developed into the glandular type. Cytokinesis during meiosis of microspore mother cells was simultaneous, with microspore tetrads typically tetrahedral, though cross-shaped microspore tetrads were occasionally observed in pollen sacs of thrum flowers. Mature pollen grains were predominantly 2-celled, with a minority being 3-celled. Regarding developmental progression, thrum flowers exhibited relatively slower microspore development but faster male gametophyte development compared to pin flowers; however, both pistils and stamens were fully mature at anthesis in both morphs. Overall, the reproductive development of the two floral morphs of common buckwheat displays numerous relatively primitive embryological features, along with some relatively derived traits such as orthotropous ovules and 3-celled pollen. This study not only enriches the morpho-cytological data on reproductive development in the two floral morphs of common buckwheat, but also provides embryological evidence for understanding phylogenetic relationships among species in the order Caryophyllales.

## Full Text

### Preamble

#### Comparative Study on the Development of Stamens and Carpels in Pin and Thrum Flowers of Common Buckwheat

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### Abstract

To elucidate the morphological differences in the development of the two floral morphs in common buckwheat (*Fagopyrum esculentum*), we employed paraffin sectioning to observe and compare megasporogenesis, microsporogenesis, and the development of female and male gametophytes in pin and thrum flowers. The results revealed high cytological similarity in pistil and stamen development between the two floral types. Both possess orthotropous ovules with double integuments and a thick nucellus. Megaspore mother cells undergo meiosis to form linear tetrads, with the chalazal megaspore being functional, developing into a Polygonum-type embryo sac. The anther is tetrasporangiate, with the anther wall comprising epidermis, endothecium, a single middle layer, and a glandular tapetum. Cytokinesis during microspore mother cell meiosis is simultaneous, typically yielding tetrahedral microspore tetrads, though occasional decussate tetrads were observed in thrum flowers. Most mature pollen grains are 2-celled, with a minority being 3-celled. In terms of developmental timing, thrum flowers showed relatively slower microspore development but faster male gametophyte development compared to pin flowers; however, both floral types achieved mature pistils and stamens at anthesis. Overall, the reproductive development of common buckwheat exhibits many relatively primitive embryological features alongside some derived traits such as orthotropous ovules and 3-celled pollen. This study not only enriches the morphocytological data on distylous reproductive development in common buckwheat but also provides embryological evidence for understanding phylogenetic relationships among species in Caryophyllales.

**Keywords:** *Fagopyrum esculentum*, pin flower, thrum flower, mega- and microsporogenesis, female and male gametophyte development

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Common buckwheat (*Fagopyrum esculentum*), belonging to the family Polygonaceae in the order Caryophyllales, is one of three cultivated species in the genus *Fagopyrum* (Tang et al., 2019). It is an economically important plant with multiple uses as food, medicine, ornamental, and soil remediation. Buckwheat grains contain higher levels of protein, fiber, and trace elements than rice, wheat, and corn, and are rich in flavonoids such as rutin, quercetin, and kaempferol, offering high nutritional value and health benefits. As a functional

food crop, it has attracted increasing attention in recent years (Joshi et al., 2019; Zhang et al., 2020; Zhang, 2020; Huda et al., 2021). However, as a typical distylous plant, natural populations of common buckwheat segregate short-styled long-stamen (thrum) and long-styled short-stamen (pin) morphs at a 1:1 ratio, with successful seed set occurring only through reciprocal pollination between stigmas and anthers at equivalent heights (Plate I). This low yield and difficulty in hybrid breeding have severely limited the promotion of this important crop. Since grain is the primary product organ, its yield and quality are closely related to reproductive development. Therefore, understanding the patterns of reproductive development is crucial for guiding artificial emasculation, hybrid breeding, and quality improvement in common buckwheat.

Previous studies on buckwheat reproductive development have focused on exogenous hormone regulation of floral bud differentiation (Jin et al., 2019), pericarp dehiscence types and their effects on early germination traits (Li et al., 2020), hybridization patterns between isostylous resources and cultivated varieties (Chen et al., 2020), and molecular mechanisms regulating pistil, stamen, and perianth development (Li et al., 2017; Liu et al., 2019; Zhang et al., 2021). Research on heterostyly differentiation has primarily addressed the genetics and genomics of heteromorphic self-incompatibility, breeding applications, and molecular mechanisms of distylous development (Barrett, 2019; Matsui & Yasui, 2020), while morphocytological data on distylous flower development remain scarce.

This study compares the morphocytological processes of pistil and stamen development between pin and thrum flowers in common buckwheat. By analyzing the similarities and differences in megasporogenesis, microsporogenesis, and gametophyte development, we aim to enrich the morphocytological documentation of distylous reproductive development and provide embryological evidence for understanding evolutionary relationships within *Fagopyrum* and across Caryophyllales.

**Plate I.** Flower types of *Fagopyrum esculentum*

A: Thrum flower (short pistil, long stamen); B: Pin flower (long pistil, short stamen)

## 1. Materials and Methods

### 1.1 Plant Materials

In early September 2019, plump seeds of the common buckwheat cultivar ‘Beizaosheng’ were sown in plastic pots (21 cm × 14 cm × 20 cm) at the Crop Genetics and Breeding Research Base of Yangtze University under conventional fertilizer and water management. When inflorescences began to differentiate and develop, the fastest-developing inflorescences from plants at different leaf stages were immediately fixed in FAA solution [V(formalin):V(glacial acetic acid):V(70% ethanol) = 1:1:18] and stored at 4°C.

## 1.2 Experimental Methods

Floral differentiation in 'Beizaosheng' buckwheat was first observed when the third true leaf began developing on the main stem, with the first flowers typically opening in the axillary inflorescences of the fourth true leaf. Sampling therefore commenced at the third-leaf stage. One hundred twenty plants were randomly selected and tagged; from these, twenty plants had their apical inflorescences removed and fixed in FAA for later floral type identification after flowering. The remaining 100 tagged plants were sampled from the fourth-leaf stage onward. Each time an additional true leaf developed on the main stem, inflorescences from the fourth-leaf axil were collected from twenty randomly selected tagged plants and fixed in FAA until the first flower opened in these inflorescences. All samples were labeled for floral type determination after flowering.

Typical inflorescence samples representing each developmental stage were selected for both pin and thrum flowers. At each stage, three inflorescences were randomly chosen and pooled in fresh FAA solution. After dehydration, samples were rinsed three times in 50% ethanol, then dehydrated through an ethanol series (70%, 85%, 95%, 100%), two hours per step. Clearing was performed in 1/2 ethanol + 1/2 xylene followed by 100% xylene, two hours each. For paraffin infiltration, materials were first placed in paraffin-saturated xylene at 38°C for 15 hours, then transferred to pure liquid paraffin at 68°C for 12 hours with paraffin changes every 4 hours. After embedding, 8  $\mu$ m sections were cut using a Leica RM2235 microtome (Li, 1996). Sections were double-stained with 1% safranin and 0.1% fast green, mounted in Canada balsam, and observed under a Caikon RCK-40C microscope.

## 2. Results

### 2.1 Microsporogenesis and Male Gametophyte Development in Pin Flowers

In pin flowers, inflorescence differentiation began when the third true leaf developed on the main stem. At this stage, some floral buds showed nearly rectangular anthers with conspicuous microspore archesporial cells at the corners; some archesporial cells had undergone periclinal division to produce parietal cells adjacent to the epidermis and inner sporogenous cells (Plate II: A). When the fourth true leaf developed, microspore mother cells were observed in some buds, with anthers being tetrasporangiate and butterfly-shaped. Parietal cells had divided periclinally to form endothecium, middle layer, and multinucleate tapetum (Plate II: B). In some buds, microspore mother cells showed intercellular spaces and began meiosis, with clear gaps in multinucleate tapetum cells (Plate II: C). In more advanced buds, microspore mother cells completed meiosis to form tetrahedral tetrads after nuclear division (Plate II: D, E).

When the fifth true leaf developed, microspore tetrads in some buds began to dissociate into uninucleate microspores, with asynchronous development among different pollen sacs. The middle layer had disappeared, and multinucleate

tapetum further degenerated, creating visible gaps with the endothecium (Plate II: F). At the sixth-leaf stage, uninucleate microspores showed increased volume, thickened walls, and a large central vacuole, with the nucleus moving to one side to form the uninucleate peripheral-stage microspore. The multinucleate tapetum dissolved adjacent to the endothecium, leaving some residues, while epidermal cells darkened (Plate II: G). When the seventh true leaf developed, 2-celled pollen grains formed (Plate II: H), with occasional 3-celled pollen grains also observed (Plate II: I).

**Plate II.** Microsporogenesis and development of male gametophytes in pin flowers of common buckwheat

A: Microspore archesporial cell, parietal cell, and sporogenous cell; B: Microspore mother cell; C: Microspore mother cell beginning meiosis; D: Telophase II of microspore mother cell meiosis; E: Tetrahedral microspore tetrads; F: Microspores releasing from tetrads; G: Monokaryotic microspore with nucleus located aside; H: 2-celled pollen grains; I: 3-celled pollen grains

## 2.2 Megasporogenesis and Female Gametophyte Development in Pin Flowers

When the fourth true leaf developed on pin flower plants, some floral buds showed a conspicuous, large-nucleated megaspore archesporial cell differentiating beneath the nucellar epidermis (Plate III: A). In some buds, the archesporial cell divided periclinally to produce a parietal cell and a sporogenous cell (Plate III: B). In more advanced buds, the sporogenous cell enlarged to become the megaspore mother cell (Plate III: C, D). At the fifth-leaf stage, megaspore mother cells began meiosis while the outer integument started developing (Plate III: E). When the sixth true leaf developed, megaspore mother cells completed meiosis to form linear tetrads (Plate III: F). In advanced buds, the three megaspores distant from the chalazal end degenerated, while the chalazal megaspore developed into the functional megaspore, with the outer integument extending to the apex of the orthotropous ovule (Plate III: G).

At the seventh-leaf stage, some buds showed large, dense-cytoplasm uninucleate embryo sacs, with inner integuments beginning to converge at the apex to form the micropyle (Plate III: H). In more advanced buds, mature Polygonum-type embryo sacs were observed, with three cells at the micropylar end arranged in a triangular pattern. Two synergids near the micropyle and one egg cell near the chalaza constituted the egg apparatus, while the two polar nuclei fused to form a secondary nucleus (Plate III: I).

**Plate III.** Megasporogenesis and development of female gametophytes in pin flowers of common buckwheat

A: Megaspore archesporial cell; B: Parietal cell and megaspore sporogenous cell; C: Megaspore sporogenous cell; D: Megaspore mother cell with inner integument beginning development; E: Outer integument beginning development; F: Linear tetrad of megaspores; G: Functional megaspore; H: Uninucleate embryo sac; I:

Mature embryo sac. An: Antipodal cells; Eg: Egg cell; Sn: Secondary nucleus; Sy: Synergids

### 2.3 Microsporogenesis and Male Gametophyte Development in Thrum Flowers

Thrum flower inflorescences also differentiated when the third true leaf developed. At this stage, some floral buds showed butterfly-shaped anthers with large microspore sporogenous cells at the corners, where surrounding parietal cells showed asynchronous periclinal division (Plate IV: A). In advanced buds, distinct microspore mother cells were observed (Plate IV: B). When the fourth true leaf developed, microspore mother cells in some buds began meiosis, forming tetrahedral tetrads and occasionally decussate tetrads (Plate IV: C-F). In more advanced buds, some tetrads began to dissociate (Plate IV: G).

At the fifth-leaf stage, many irregularly shaped uninucleate microspores appeared (Plate IV: H), which subsequently increased in volume, became rounded, and developed prominent walls (Plate IV: I). When the sixth true leaf developed, microspores reached the uninucleate peripheral stage (Plate IV: J), with 2-celled pollen grains observed in advanced buds (Plate IV: K). At the seventh-leaf stage, mature pollen consisting predominantly of 2-celled pollen grains was observed (Plate IV: L).

**Plate IV.** Microsporogenesis and development of male gametophytes in thrum flowers of common buckwheat

A: Microspore sporogenous cell; B: Microspore mother cell; C: Microspore mother cell beginning meiosis; D: Meiosis I of microspore mother cell; E: Tetrahedral microspore tetrads; F: Decussate microspore tetrads; G: Microspores releasing from tetrads; H: Irregularly shaped mononuclear microspore; I: Thickened wall of monokaryotic microspore; J: Monokaryotic microspore with nucleus located aside; K: 2-celled pollen grains; L: Mature 2-celled pollen grains

### 2.4 Megasporogenesis and Female Gametophyte Development in Thrum Flowers

When the third true leaf developed on thrum flower plants, a conspicuous, relatively large archesporial cell appeared in the ovule nucellus of some floral buds (Plate V: A). At the fourth-leaf stage, archesporial cells began periclinal division (Plate V: B), producing a parietal cell and a sporogenous cell. As the sporogenous cell enlarged, the inner integument began developing (Plate V: C), and the sporogenous cell developed into the megaspore mother cell (Plate V: D). At the fifth-leaf stage, megaspore mother cells were still undergoing meiosis while the outer integument began developing (Plate V: E). When the sixth true leaf developed, megaspore mother cells completed meiosis to form linear tetrads (Plate V: F). The three megaspores near the micropylar end degenerated sequentially, while the chalazal megaspore developed into the functional megaspore (Plate V: G). In advanced buds, the three micropylar megaspores

degenerated completely, and the functional chalazal megaspore enlarged with an expanded nucleus to form a uninucleate embryo sac (Plate V: H). At the seventh-leaf stage, the uninucleate embryo sac underwent three mitotic divisions to form an 8-nucleate, 7-celled mature Polygonum-type embryo sac (Plate V: I).

**Plate V.** Megasporogenesis and development of female gametophytes in thrum flowers of common buckwheat

A: Megaspore archesporial cell; B: Archesporial cell periclinal division; C: Megaspore sporogenous cell with inner integument beginning development; D: Megaspore mother cell; E: Meiosis of megaspore mother cell with outer integument beginning development; F: Linear tetrad of megaspores; G: Functional megaspore; H: Uninucleate embryo sac; I: Mature embryo sac. An: Antipodal cells; Eg: Egg cell; Pn: Polar nuclei; Sy: Synergids

## 2.5 Comparison of Pistil and Stamen Development Between Pin and Thrum Flowers

The fundamental embryological characteristics of pistil and stamen development differed in timing between the two floral types. Compared to pin flowers, thrum flowers showed relatively slower microspore development but faster male gametophyte development. However, both floral types achieved mature pistils and stamens at anthesis. The specific developmental correlations are summarized in

**Table 1** Relationship between pistil and stamen development in pin and thrum flowers

Pin flower stamen development	Thrum flower stamen development	Pistil development
Microspore mother cell	Microspore mother cell	Megaspore archesporial cell
Microspore mother cell meiosis	Microspore mother cell meiosis	Megaspore sporogenous cell
Microspore tetrad	Microspore tetrad	Megaspore mother cell
Microspores releasing from tetrads	Microspore tetrad	Megaspore mother cell meiosis
Monokaryotic microspore with nucleus located aside 2-celled pollen	Irregularly shaped mononuclear microspore Monokaryotic microspore with nucleus located aside	Megaspore tetrad Functional megaspore
Mature pollen grains	2-celled pollen	Uninucleate embryo sac

Pin flower stamen development	Thrum flower stamen development	Pistil development
	Mature pollen grains	Mature embryo sac

### 3. Conclusion and Discussion

Thrum flowers exhibited slower microspore development but faster male gametophyte development compared to pin flowers. This may be attributed to the longer filaments in thrum flowers, which require more nutrients for elongation during microspore development. However, at the microspore tetrad stage, megaspore mother cells had already appeared in ovules of both floral types, with style development commencing. Pin flowers possess longer styles that also demand substantial nutrients, potentially slowing male gametophyte development relative to thrum flowers. Thrum flower pollen grains were slightly larger than those of pin flowers, consistent with findings by Zhang and Chen (2002). Zhang et al. (2015) reported that pin flowers set seed more readily than thrum flowers, and Sun et al. (2021) observed similar patterns in the distylous plant *Forsythia suspensa*. Our morphocytological analysis revealed that in pin flowers, polar nuclei had already fused into a secondary nucleus before anthesis, better preparing for double fertilization and providing direct morphocytological evidence for the higher pollination success in pin flowers.

Common buckwheat exhibits high embryological similarity to the self-pollinating homostylous tartary buckwheat (*Fagopyrum tataricum*). However, thrum flowers of common buckwheat predominantly show tetrahedral microspore tetrads with occasional decussate tetrads, and both pin and thrum flowers produce mostly 2-celled pollen with some 3-celled pollen—distinct from tartary buckwheat, which has only tetrahedral tetrads and exclusively 2-celled pollen (Wu et al., 2017). Among other Caryophyllales species, 3-celled pollen has only been reported in *Beta vulgaris* (Amaranthaceae) and several *Limonium* species (Plumbaginaceae) (Shen et al., 1986; Li et al., 2006; Zhou et al., 2007; Kong et al., 2008). The coexistence of tetrahedral and decussate microspore tetrads has also been observed in the core Caryophyllales species *Ceratoides arborescens* (Amaranthaceae) (Lu et al., 2008), suggesting close phylogenetic relationships among buckwheat, Amaranthaceae, and Plumbaginaceae.

Common buckwheat exhibits relatively primitive embryological traits including tetrasporangiate anthers, double integuments, thick nucellus, chalazal functional megaspores, and Polygonum-type embryo sacs (Wang, 1980). However, unlike the typical anatropous ovules common in Caryophyllales, buckwheat possesses the relatively derived orthotropous ovule type, while Plumbaginaceae shows campylotropous ovules (Hu, 2005; Li et al., 2006; Zhou et al., 2007; Kong et al., 2008), supporting the classification of Polygonaceae and Plumbaginaceae as non-core Caryophyllales—a conclusion that aligns well with molecular systematics (APG, 2016). Other Caryophyllales families also show this pattern of

predominantly primitive embryological features with some derived traits. For example, core Caryophyllales species *Phytolacca americana* and *P. acinosa* (Phytolaccaceae) exhibit primitive features like tetrasporangiate anthers, anatropous ovules, double integuments, thick nucellus, chalazal functional megaspores, and Polygonum-type embryo sacs, but produce only three megaspores (triads) after meiosis (Xin et al., 2000; Li et al., 2015). The non-core Caryophyllales species *Tamarix chinensis* (Tamaricaceae) shows primitive traits like double integuments, thick nucellus, and anatropous ovules alongside derived features including numerous ovules and Fritillaria-type embryo sacs (Wang et al., 2005).

In summary, pin and thrum flowers of common buckwheat show substantial similarity in megasporogenesis, microsporogenesis, and gametophyte development, with notable differences in developmental timing. Thrum flowers exhibit slower microspore development but faster male gametophyte development, and occasionally produce decussate microspore tetrads unlike the exclusively tetrahedral tetrads in pin flowers. Comparative embryological analysis across Caryophyllales reveals that while most species display relatively primitive embryological features, derived traits such as 3-celled pollen, orthotropous and campylotropous ovules, megaspore triads, and Fritillaria-type embryo sacs also occur, reflecting the complex evolutionary history of this order.

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