



Morphological and anatomical changes during floral bud development of the trioecious *Idesia polycarpa* Maxim

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Abstract

Idesia polycarpa Maxim is described as a dioecious species, in which flowers are female or male, but we have also found individuals with bisexual flowers. The study aimed to provide the theoretical basis for the artificial control on flowering, fruiting, and floral initiation of *Idesia polycarpa* Maxim species. The morphological and anatomical structure of female, male, and bisexual flowers of *I. polycarpa* was studied. In this study, the routine paraffin section and morphological observation methods were used. The flowering of *I. polycarpa* began in late July. Results showed that the short-branch terminal bud was the highest percentage of floral bud position both in the female and male plants compared to the other bud types, and the proportion was 68.6% and 76.3%, respectively. Evidence from floral structural analysis suggests that the female and male flowers of *I. polycarpa* are unisexual by abortion. The ovary of the male flower stops developing after the ovule primordium initiation. The female, male, and bisexual flowers of *I. polycarpa* had the same anatomical structure at the beginning of development, but differences emerge in the differentiation stage of the female and male. In the bisexual flowers, females and males develop normally and may produce fruits. The study suggests that the bisexual, male, and female flowers were produced on the separate plants of the same species; therefore, the species is trioecious.

Keywords Bisexual flower · *Idesia polycarpa* · Sex conversion · Trioecy · Type I flowers

1 Introduction

Idesia polycarpa Maxim is described as a dioecious species that belongs to the family of Flacourtiaceae. The species is indigenous to Asia and widely distributed in China, Korea, and Japan (Bernhard and Endress 1999; Chen et al. 2019). The *I. polycarpa* fruit oil possesses high values in edible properties, health care, medicinal, and producing biodiesel (Yang et al. 2009; Jung et al. 2010; Lee et al. 2013; Dai 2014). During the seedling stage, the plant sex is hard to distinguish between female and male plants and takes around 4 or 5 years to reach reproductive maturity (Chen et al. 2019; Rana et al. 2022). In addition, only the female plants can produce fruits, which causes difficulties in the high-yield cultivation of this species. Hence, it is important to identify the sexual type and regulate sex differentiation

as early as possible. The sex differentiation of plants is a critical and complicated morphogenesis process, which is being influenced by internal and external factors, such as phytohormone, genetic, epigenetic, and environmental factors (Aryal and Ming 2014; Pan et al. 2016; Akagi et al. 2018). Therefore, studying the morphological variations of floral bud differentiation is the basis for identifying and regulating the sex differentiation of *I. polycarpa*.

The *Idesia polycarpa* Maxim flowers are unisexual, and the female flower is smaller than the male flowers. The female flower comprises calyx, pistil, and vestigial stamens (staminodes), and the male flower has calyx, stamens, and reduced pistillodes (Mei et al. 2017). In the previous observations of our study group (not published), we found that there were some *I. polycarpa* plants with bisexual flowers. The types of sexuality in individual flowers are female, male, and hermaphrodites, respectively. The stamens and carpels of the bisexual flowers both grow normally.

In the angiosperms, dioecism is uncommon, with in-depth field investigation; it has been discovered that the

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plants which are considered being dioecious have gender transitions. Besides the female and male plants, there are trioecious plants, trioecism is rare and the frequency of trioecious sexual phenotype in the angiosperms is less than 1.0% (Cruden and Lloyd 1995). An male *Ginkgo* plant possesses a localized sex conversion branch that could produce viable seeds, but the abundant cones of the *Ginkgo* plant were morphologically male (Nagata et al. 2016). Some *Diospyros* species exhibited leaky dioecy, and the results showed that some leaky male *Diospyros* plants could produce viable seeds (Venkatasamy et al. 2007). There were no significant differences in the germination rates of seeds from hermaphroditic and female individuals. There are also bisexual variants, in which both stamens and pistils can grow normally (Wang et al. 2012; Gu et al. 2020). However, the reason for the emergence of bisexual variants in dioecious species is still unclear, and the morphology of *I. polycarpa* bisexual flowers has not being reported.

The main purpose of this study was to describe the floral morphology and anatomy of the male, female, and bisexual flowers at the different developmental stages, aiming to provide the theoretical basis for *I. polycarpa* floral organ development and lay the foundation for a better understanding of the sex system evolution in angiosperms.

2 Materials and methods

Study site – This study was undertaken at the experimental research station (112° 42' 114° 14' E, and 34° 16' 34° 58' N), College of Forestry, Henan Agricultural University, Zhengzhou, Henan Province, China, in 2018–2019. The mean annual temperature of this site is 14.2 °C, the frost-free period is 215 days, the mean annual precipitation of 650.1 mm, annual sunshine hours are about 2400 h, and the soil is slightly alkaline sandy loam (Rana and Liu 2021; Rana et al. 2022).

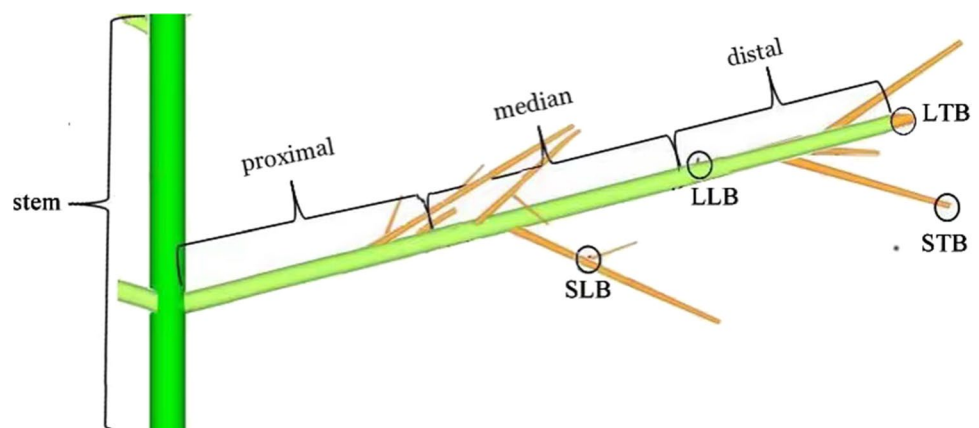
Plant materials and data sampling – This study was conducted on the 5-year-old *I. polycarpa* Maxim plants. A total of 23 plants were sampled (10 females, 10 males, and 3 bisexuals). The period of the experiment was from July 2018 to late April 2019. One or two branches were selected from the female and male plants; the samples and the static images of the terminal buds (TB) and lateral buds (LB) were recorded every 10 days from July 2018 to February 2019. In addition, the female, male and bisexual floral buds were being sampled and static images were being recorded every 5 days during the floral buds germinating to the blossoming stage (March 2019 to late April 2019).

The observation has begun two weeks before the sprouting season of the TB and lateral buds (LB). The different types of branches and buds were demonstrated in the diagram of the *I. polycarpa* model branch (Fig. 1). The branches that are emerging on the stem are considered as long branches, short branches emerge from the long branches, with a length of over 5 cm. In this study, we divided the long branches into three sections: proximal, median, and distal.

The samples of floral buds, inflorescences, and florets were collected from female, male, and bisexual plants at different development stages and fixed in FAA 50, thereafter dehydrated in a normal ethyl alcohol series, and embedded in paraffin following the standard protocol. The embedded materials were sectioned at 7 µm, with sections being stained with safranin/fast green. Digital image scanner technique (3D HISTECH panoramic SCAN) and digital images processing software (Case Viewer) were adopted to analyze the anatomical structure.

Statistical analysis – Due to the limited of bisexual floral buds, the comparison was not made with the other (female and male) sexes. We analyzed the differences of female and male plants floral bud numbers, using Excel v. 2016 (Microsoft Corp., Redmond, WA, USA) to do statistical analysis. The rate of floral bud differentiation with the particular branch type of female and male plants was calculated. The

Fig. 1 Illustration of the model branch most commonly being found in *I. polycarpa* plants. The proximal, median, distal sections indicate different parts of the long branch. STB, short-branch terminal buds; LTB, long-branch terminal bud; LLB, long-branch lateral bud; SLB, short-branch lateral bud



biological meaning of the percentages of floral buds with the particular branch type is to provide foundation work for regulating the sex differentiation of *I. polycarpa* male plants at the inflorescence differentiation stage, because of that, the male plants have the sex conversion phenomena. The calculation formula of floral bud differentiation is as follows:

$$\text{Percentages of floral buds with particular branch type} = \frac{\text{The number of floral buds with particular branch type}}{\text{Total floral bud numbers}} \times 100.$$

3 Results

Floral bud pattern – The position and number of the newly sprouting floral buds on female and male plants were counted. The floral buds of short branch terminal buds (STB) held the highest proportions both in female and male plants among the long-branch terminal bud (LTB), long-branch lateral bud (LLB), and short-branch lateral bud (SLB). The proportion was 68.6% and 76.3% in female and male plants, respectively. The number of flower buds on the short branches in female and male plants was more than that of long branches, and the proportion was 86.3% and 89.5%, respectively.

Morphological and anatomical aspects of floral buds – The morphology of STB in the female and male plants was observed from July 2018 to March 2019 (Figs. 2, 3). In July, most of the female and male STB were small and tender green, whereas, in September the color of the buds turned tan to brown, with fasciculate hairs. The leaves of both sexes

were fell off in December, and with leaf scars in the twig. The terminal buds were in the dormant state and protected by bud scales. The scales fell from the buds at the initiation of the sprouting season in March 2019, and the buds get ready to resume growth when it gets warm again, after about 10 leaves were formed (middle-to-late March). During this period, the inflorescence could be seen in the buds. There was no significant difference in the morphology of flower buds at different locations (distal, median, and proximal) between the female and male *I. polycarpa* plants from July 2018 to February 2019. The difference between the female and male floral buds appeared, and the bud scales of male flower buds cracked earlier than female flower buds (Figs. 2, 3).

The morphology of female, male, and bisexual inflorescence of *I. polycarpa* and the three types of inflorescences



Fig. 2 Morphological aspects of short-branch terminal buds of *I. polycarpa* male plants. The static images are short-branch terminal buds from the distal (a–f), median (g–l), and proximal (m–r) parts of the long branch in July 2018, September 2018, December 2018, early March 2019, middle and late March 2019



Fig. 3 Morphological aspects of short-branch terminal buds of *I. polycarpa* female plants. The static images are short-branch terminal buds from the distal (a–f), median (g–l), and proximal (m–r) parts of the long branch in July 2018, September 2018, December 2018, early March 2019, middle and late March 2019

are composed of lateral branches and pedicels on the branches; the calyx color of the three types of inflorescences is yellow-green, no petals (Fig. 4a–d). The shape, floret size, and pedicel length of bisexual inflorescence (Fig. 4b) are like those traits of male inflorescence (Fig. 4c). The morphology of flower buds between the male and bisexual plants could not be distinguished before blooming. In the longitudinal section view of the female, male, and bisexual flowers (Fig. 4h), it can be seen that the calyx of *I. polycarpa* is synsepalous, with the proximal region united and the distal region-free. The androecium of male flowers is distinct stamens, with a pistillode, which was reduced and shriveled (Fig. 4g). The gynoecium of the female flower is syncarpous; the ovary and style are united, with the plicated stigmas (Fig. 4e). The staminodes of the female flower have short filaments and antherode with no pollen. The stamens and carpels of bisexual flowers both develop. The carpel in bisexual and female flowers has the same morphological traits; both of them can develop into fruits. The stamens in bisexual flowers and male flowers have the same morphological characteristics and also can produce pollen (Fig. 4f).

In early July, the shoot apical meristem (G, growth cone) of the female and male buds was sharp and narrow. In late July, the growth cone had turned flat, which is a sign of the transition from vegetative development to reproductive development. The floral meristem produced in the regions of shoot apical meristem is also called inflorescence meristem

after floral transition (Fig. 5). In late September, the floral meristems of the female and male plants continue to develop into leaf primordia, after then, the buds are in a dormant state at the end of the growing season. Until mid-March 2019, the inflorescence meristem of female and male floral buds continued to elongate at the initiation of the sprouting season. In mid-March 2019, bract primordia appeared in the inflorescence meristem of male plants, while the female plants did not differentiate into bract primordia. The male inflorescence meristem differentiated earlier than female plants. The differences of female and male bud's longitudinal sections appeared in mid-March 2019 (Fig. 5). After the sprouting season, the floral buds of females and males both were in the great elongating stage. In late March, the male floral buds were in the stamen primordium differentiation stage, but the stamen primordium of female floral buds did not develop, which were at the bract primordia development stage, which was consistent with the observation results of the external morphology of female and male floral buds (Fig. 6).

Morphological and anatomical aspects of flowers – The anatomical structure of female, male, and bisexual flowers was similar at floral organ differentiation early stage (early April). The three types of flowers produce carpel and stamens at the early stage of floral differentiation (Fig. 7a–c). The gynoecium and stamens develop normally in the

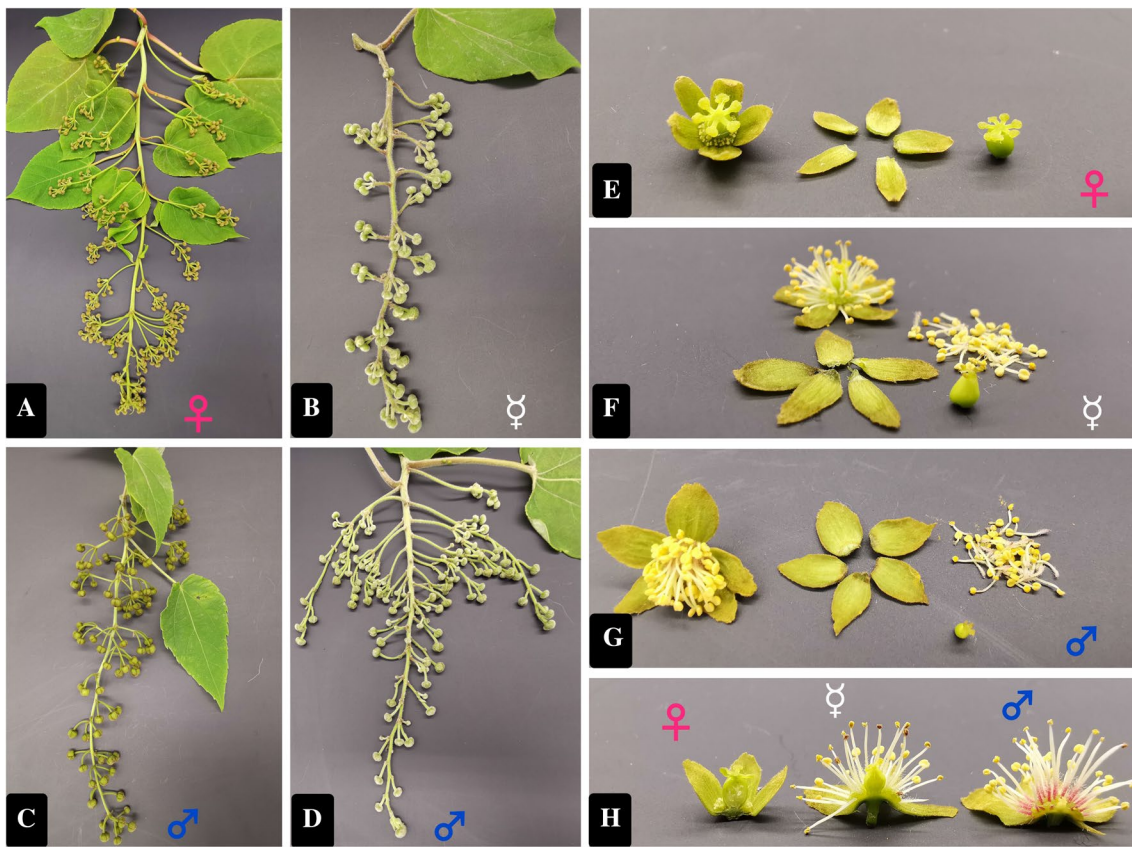


Fig. 4 The identification of static images by the uppercase letters. The full form of the letters is as follows: **A** female inflorescence; **B** bisexual inflorescence; **C, D** male inflorescence; **E** female flower; **F** bisexual flower; **G** male flower; **H** female, bisexual and male flowers

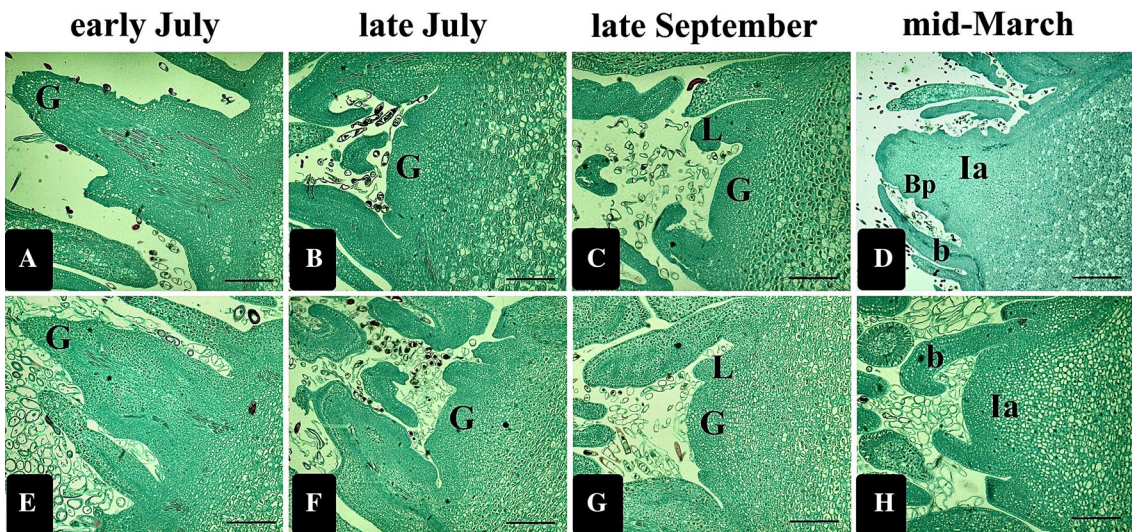


Fig. 5 Photomicrographs of longitudinal sections of *I. polycarpa* female and male floral buds. The male floral buds (**a–d**) and the female floral buds (**e–h**) in early July 2018, late July 2018, late September 2018, and mid-March 2019. The abbreviations of the uppercase and lowercase letters: G, growth cone; L, leaf primordia; Ia, inflorescence axis; b, bract primordia. Bars, 500 μ m

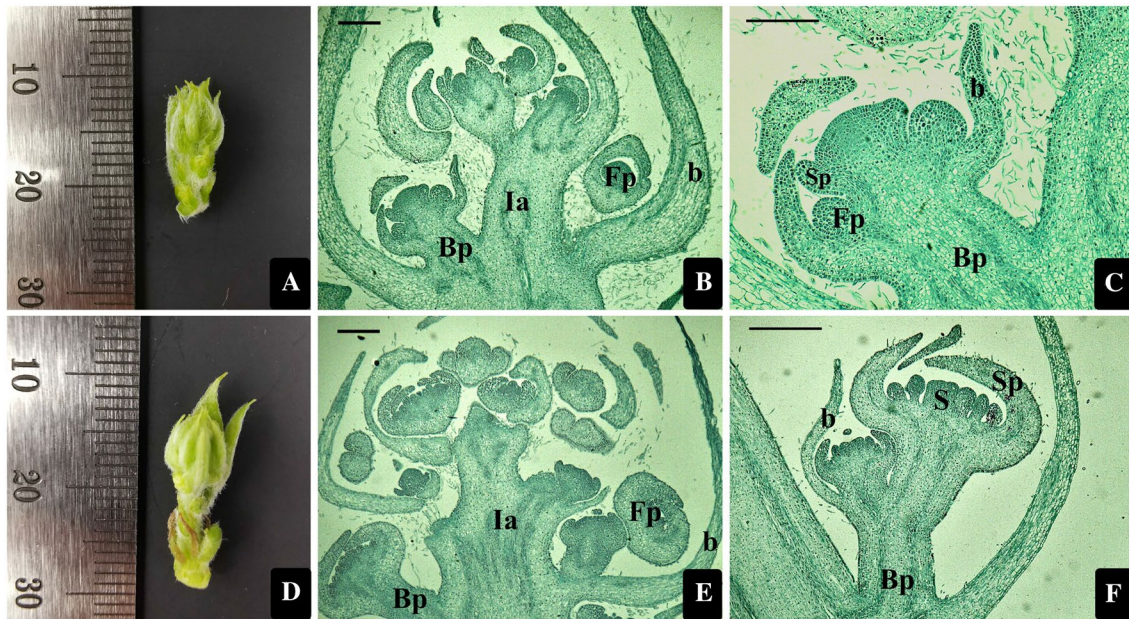


Fig. 6 The morphologic structure and longitudinal sections of *I. polycarpa* female, male floral bud in late March. The static images of female (a–c) and male (d–f) floral bud in late March. The abbreviations of the lowercase letters: Ia, inflorescence axis; b, bract primordia; Bp, branch primordia; Fp, floral primordia; Sp, sepal primordia; S, stamen primordium. Bars, 500 μ m

bisexual flowers (Fig. 7e, h, k). While stamens in female flowers (Fig. 7d, g, j) and gynoecium in male flowers (Fig. 7f, i, l) both degenerate at late developmental stage (mid-April) and finally form unisexual female and male flowers, the abortion of the ovary of the male flower stops developing and degenerates after differentiation and development into ovule primordia (Fig. 7f) until the stamens developed to the stage of microspores. The ovules (Fig. 7i, l) in the ovary condense into a mass of subcellular components. The stamens in the female flowers stop developing before the tetrad stage. No normal pollen grains can be produced. Cavities are formed in the anther chamber; lately, the cavities were also shrink (Fig. 7d, g). The gynoecium and stamens of bisexual flowers can differentiate and develop normally in the whole floral development process (Fig. 7b, e, h, k), anthers can form pollen grains, and the ovary and ovules can develop normally and form fruits.

The anthers of *I. polycarpa* flowers contain four microsporangia (Fig. 8i). The anther walls comprise four layers: epidermis, endothecium, middle layer, and tapetum (Fig. 8a, e, i). Tapetum cells in young anther locules are arranged neatly and closely to microspore mother cells (Fig. 8f), providing nutrition for pollen development. The tapetum degenerated and disappeared, along with parts of endothecium cells persisted and became a pillar and fibrous after pollen mature (Fig. 8h, j, k). The cells being indicated (Fig. 8g, j) by the red arrow were the microspore at the tetrad stage; the microspores were released from the microspore tetrads after the meiosis II (Fig. 8h, k). In the early development stage,

the anther wall and microspore mother cells were of similar color and shape among the three types of flowers (Fig. 8a, e, i). The results showed that the microspore mother cells of female flowers abortion occurred before the meiosis stage, after that, the microspore mother cells compressed and broke down. The chromatin was in the high agglutination state (Fig. 8c) and eventually degenerated (Fig. 8d). The cytological characteristics of color and shape of bisexual anther cells were similar to male anther cells. Eventually, both male and bisexual flowers could release mature pollen (Fig. 8h, k).

The ovules of *I. polycarpa* female, male, and bisexual flowers were similar in morphology in the early development stage; all of them had the ovule primordium in the ovary (Fig. 9a, d, g). The anatomy of ovules showed the bitegmic ovule (Fig. 9b). During the ovule primordium to mature ovule development, the cytological feature of bisexual flowers was like female flowers; the ovules of female and bisexual flowers both could develop normally (Fig. 9c, i). The ovule primordium of male flowers aborts early, the cytological result showed that the abort ovules were lysed and condensed, ultimately, ovules failed to develop into seeds (Fig. 9f).

4 Discussion

Among the four floral bud positions of *I. polycarpa*, the STB of female and male plants was the highest percentage. The differentiation process of female and male flower buds in

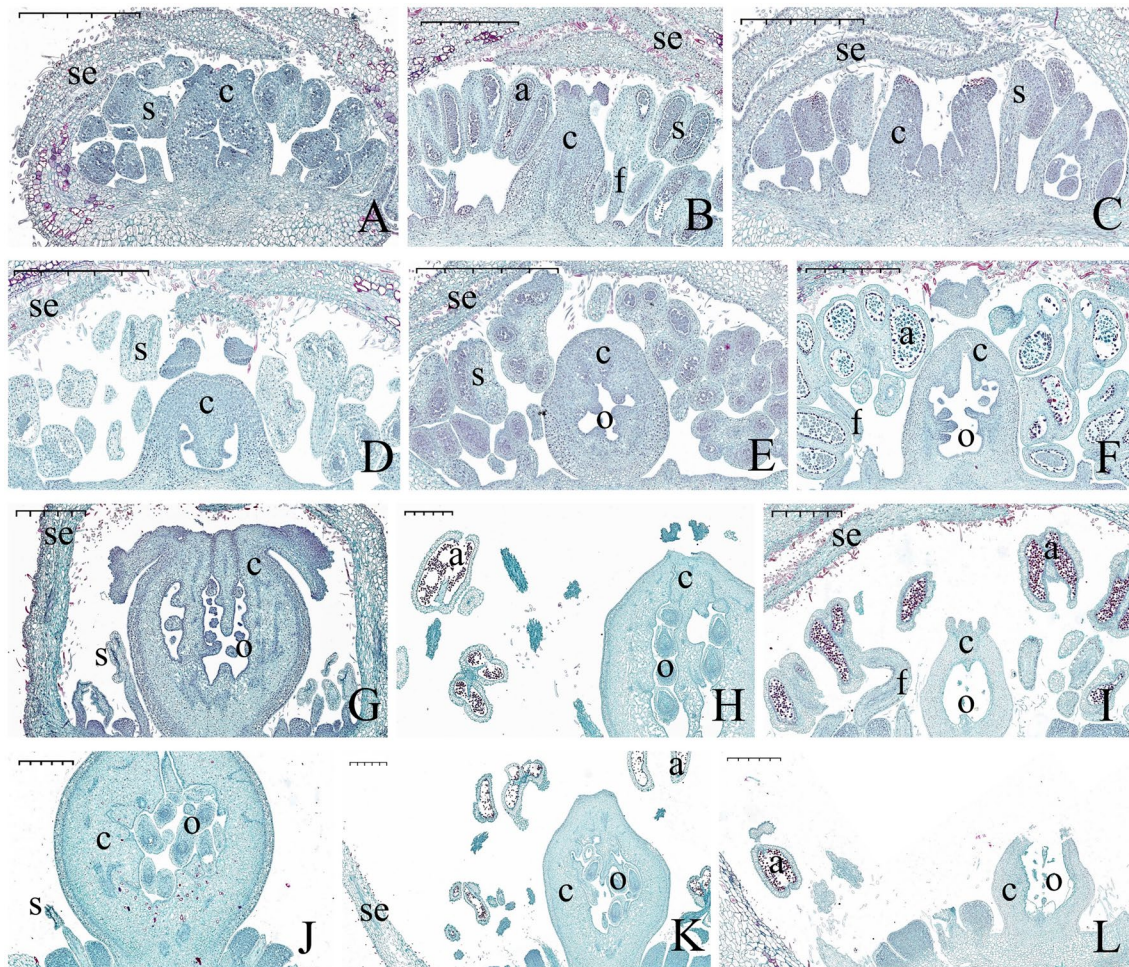


Fig. 7 Photomicrographs of longitudinal sections of *I. polycarpa* female, male, and bisexual flowers. The female (a, d, g, j), bisexual (b, e, h, k), and male flowers (c, f, i, l). The abbreviations of the lowercase letters: se, sepal; s, stamen; c, carpel; f, filament; a, anther; o, ovule or ovule primordium. Bars, 500 μ m

different positions (proximal, median, and distal) was consistent. The morphological difference was not obvious until the flower buds sprouted in the middle of March. In addition, the differentiation time of male florets is earlier than that of female florets. The morphological characteristics of bisexual flowers are similar to male flowers, the ovary of the bisexual flower was slightly smaller than the female flower, and typically it can develop into fruits. In this study, according to the internal microstructure of the female and male flower buds of *I. polycarpa*, the time of floral meristem formation was in late July. Rana and Liu (2021) reported that the elongation of terminal buds of female and male plants did not increase after July in Zhengzhou of China, which may be the key period for the transformation from vegetative growth to reproductive growth. Besides, the phenological observation of *I. polycarpa* flower in northern China was observed by Zhang et al. (2015). The phenophase of fluorescence differed

from that in central China, Zhengzhou, and the differences were because of the specific observation area.

In angiosperms, only about 6% (15,600 species) are reported to be dioecious (Kersten et al. 2017), such as poplar (*Populus*) and spinach (*Spinacia oleracea*). The widespread view that all dioecious species have evolved independently from hermaphrodite ancestors suggests that the actual developmental evolution required multiple steps across the multiple lineages, which are thought to have evolved 900–5000 times in developmental transformation (Charlesworth and Charlesworth 1978; Dellaporta and Calderon-Urrea 1993; Brunet and Charlesworth 1995; Baránková et al. 2020). According to the observation of *I. polycarpa* three types of flowers in different plants, the *I. polycarpa* andromonoecious tree could have bisexual flowers, which suggests that it's still in the dioecious developmental evolution period. The emergence of unisexual flowers results from sterile mutation or termination of the development of the reproductive organs

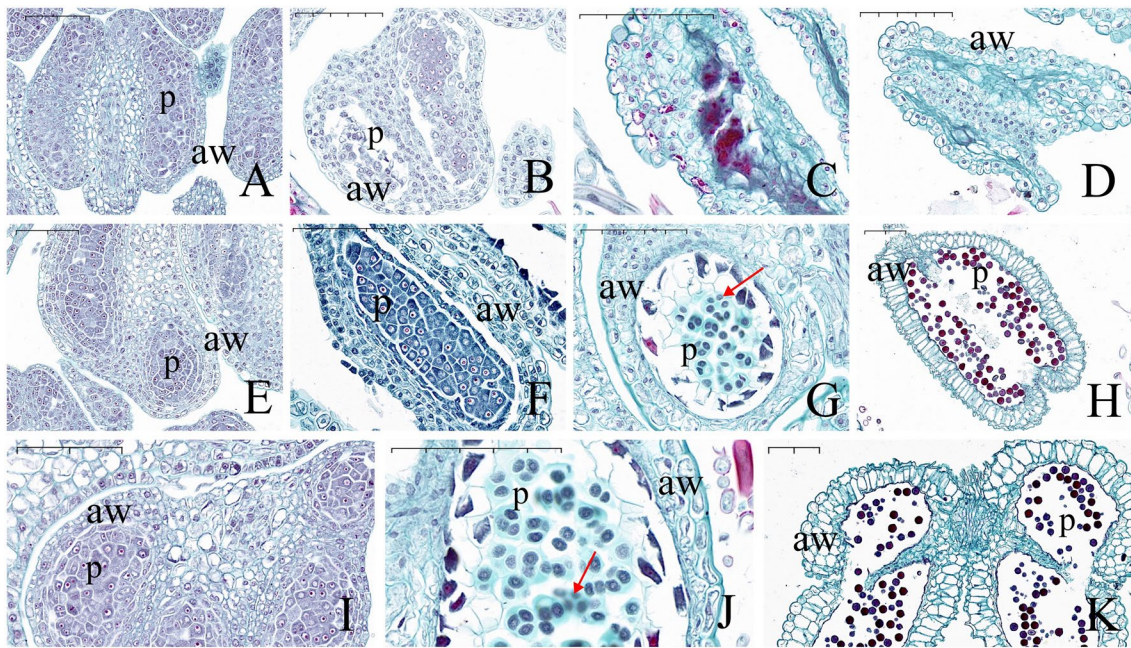


Fig. 8 Photomicrographs of longitudinal sections of *I. polycarpa* female, male, and bisexual anthers. The female (a–d), male (e–h), and bisexual flowers (i–k). The abbreviations of the lowercase letters: aw, Anther wall; p, Pollen or microspore mother cell, the red arrowheads indicate microspore tetrads. Bars, 100 μ m

(androecium or gynoecium). Historically, two broad categories of unisexual flowers have been recognized: type I flowers (unisexual by abortion) and type II flowers (unisexual from inception) (Mitchell and Diggle 2005). In flowering plants, the arrest occurs during the sexual organ development period leaving the vestige of the opposite reproduction organ, which is called unisexual by abortion (Heslop-Harrison 1958). The abortion occurs during the floral meristem cell specification stage; no stamen or carpel primordia is produced that is called unisexual from inception (Heslop-Harrison 1958).

According to the observation of external morphology and internal microstructure of *I. polycarpa* female and male flowers, the formation of unisexual flowers results from the abortion of the opposite sex organ; therefore, the female and male flowers belong to type I flowers. The arrest of reproductive organs development could occur at many stages (Ainsworth 2000). The recognition of the four stages of sexual organ abortion: Stage 0—before initiation of stamen or carpel primordia; Stage 1—early stamen or carpel development; Stage 2—pre-meiosis; and Stage 3—post-meiosis (Diggle et al. 2011). The ovule primordia of the *I. polycarpa* male flower developmental arrest occurs in the early development period, belonging to sexual organ abortion stage 1; the androecium of the female flowers abort before meiosis, which belongs to stage 2; the development of the bisexual flowers with both functional stamens and pistil. Compared with animals, sex determination in plants appears later, many

of them are still in an early evolutionary stage (Mitchell and Diggle 2005; Harkess et al. 2017). The most common sexual types are hermaphrodite, monoecy, and dioecy, besides, there are also gynodioecy, andromonoecy sexual types (Baker and Cox 1984; Krizek and Fletcher 2005; Zhang et al. 2014; Pannell 2017), the gynodioecious plants mean that the plant bears bisexual and female flowers, the andromonoecious plants mean that the plant bears bisexual and male flowers. Through continuous observation for many years, it was found that the bisexual, male, and female flowers were produced on the separate plant of *I. polycarpa*, and therefore, the tree belongs to trioecious species.

However, many mechanisms control sex differentiation in flowering plants; Zhang et al. (2015) used 200 mg L⁻¹ auxins treated *I. polycarpa* male plants at the inflorescence differentiation stage; the results showed that the treatment didn't change male flowers into the female, which may be related to the phytohormone concentration and the treatment time of auxin. The ovule primordium of *I. polycarpa* male flowers was aborted at the early carpel development stage.

Therefore, the treatment of promoting the differentiation of bisexual buds of the male plants should be carried out before the ovule primordium abortion stage. It is still unknown whether the formation of bisexual flowers is controlled by gene mutation, endogenous growth hormone, or external environmental factors in andromonoecious and bisexual plants of *I. polycarpa*. In this study, because of the limitation of bisexual flowers, only the morphological

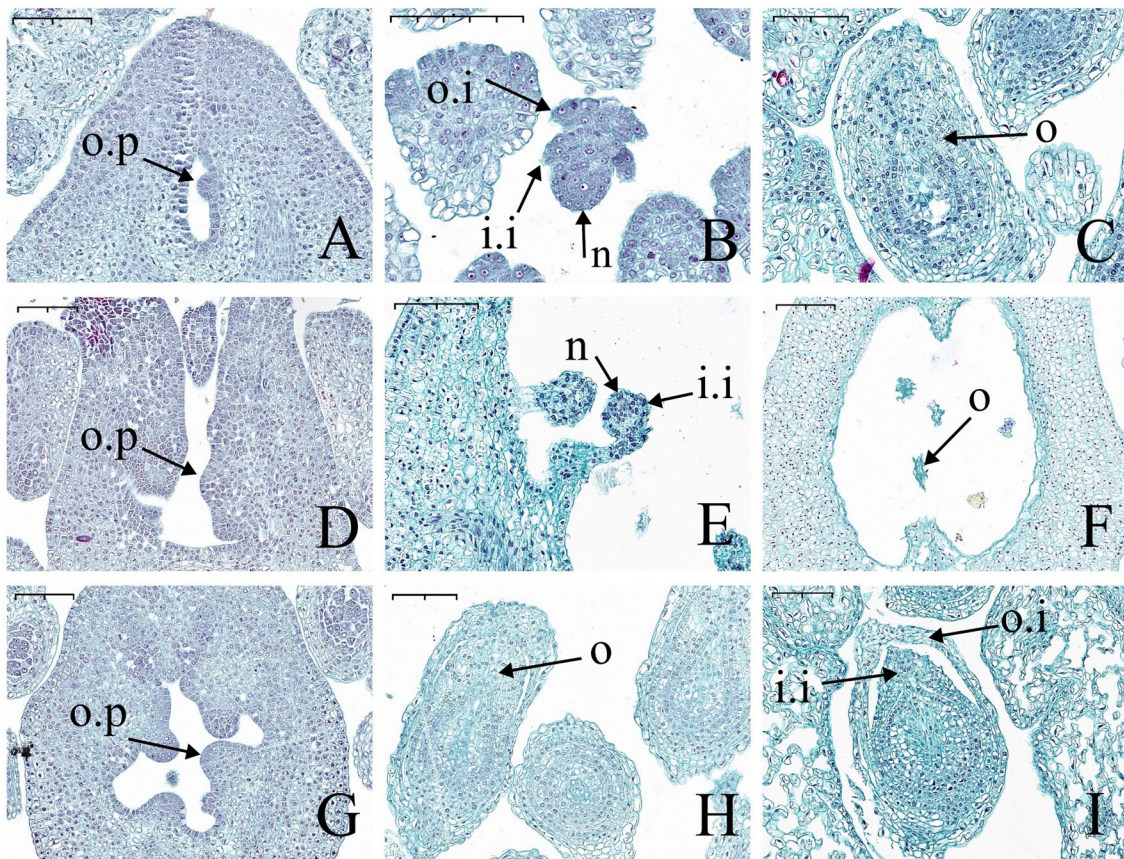


Fig. 9 Photomicrographs of longitudinal sections of *I. polycarpa* female, male, and bisexual ovules. The female (a–c), male (d–f), and bisexual flowers (g–i). The abbreviations of the lowercase letters: n, nucellus; i.i, inner integument or inner integument primordium; o.i, outer integument or outer integument primordium; o.p, ovule primordium; o, ovule. Bars, 100 μ m

and anatomical characteristics were studied. The principles that underlie the transition from male to bisexual flower have not been investigated and hence required further investigation and analysis of the sex conversion of *Idesia polycarpa* Maxim.

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Authors' contribution H.W. and Z.L. designed the experiment; H.W., Z.L., X.G., Y.W., Q.C., S.L., and J.S. carried out the experiment and analyzed the data; W.H. and S.R. drafted and revised the manuscript; Z.L. and S.R. critically revised the manuscript. All authors have read and approved this manuscript.

Data availability statement The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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