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DEVELOPMENT OF FLOWER ORGANS IN COMMON LILAC (*SYRINGA VULGARIS* L.) CV. MME FLORENT STEPMAN

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Studies on the development of common lilac cv. Mme Florent Stepman inflorescence buds and flowers were carried out in 2001–2002 in order to observe the development of flower organs before and after winter dormancy during the following phenological phases: inflorescence bud swelling, inflorescence elongation, flower bud whitening, flower bud swelling and flowering anthesis. The hypogynous, actinomorphic and perfect flower conforms to the general pattern of the Oleaceae. The calyx is four-lobed, and the four-lobed corolla is gamopetalous with a cylindrical basal tube. Two stamens are basally fused with the corolla. The anthers are tetrasporangiate, with a uniseriate epidermis, bilayered endothecium, single middle layer, and secretory, binucleate tapetum. Microspore tetrads are isobilateral and the pollen grains are spherical, three-colpate and two-celled. The ovary is superior and bilocular. Four anatropous, unitegmic and tenuinucellar ovules are formed. The female gametophyte development is Polygonum-type. Flower primordia differentiation starts in midsummer and lasts until autumn. Before entering dormancy, microspore meiosis was discernible in flowers in the lower part of the inflorescence. The ovular primordia differentiate after winter dormancy. During inflorescence bud breaking after winter dormancy, pollen mother cells in anthers and ovule primordia were observed. During inflorescence elongation, pollen mother cell meiosis and microspore tetrads occured in anthers, and the archesporial cell of the megaspores was present in ovules. During flower bud whitening and flower bud breaking, young microspores were observed in anthers, and developing megaspores were visible in ovules. In the last phenological phase, anthers dehisced and the female gametophyte was organized.

Key words: *Syringa vulgaris* L., inflorescence, flower bud, ovule, female gametophyte, pollen grains.

INTRODUCTION

In central Poland, in natural conditions the common lilac opens its flowers in the middle of May, and flowering continues to the end of May. Its flowering period is short compared to flower formation, which starts in the previous summer. In autumn (late October), preformed floral buds enter dormancy. In spring, the buds are released from deep winter dormancy and differentiation resumes. Studies of trees grown in temperate climate showed that differentiation of flower organs continues through two growing seasons (Steeves et al., 1991; Reinoso et al., 2002). Flower organ development is completed in six to eight weeks during the spring following the year of initiation. In *Amelanchier alnifolia* buds in Saskatoon (Canada), formation of the sepals, petals, sporogenous tissue of stamens and carpels lasts from July to September (Steeves et al., 1991). In April, once deep dormancy is over, pollen mother cells are observed. Pollen grains are formed during the first days of May. The stylar transmitting tissue and papillate stigmatic surface are formed in April, and the ovules differentiate in April-May. Pollination occurs in May. Findings on the timing of anatomical changes were similar in *Prunus persica* buds grown in Argentina (Reinoso et al., 2002).

Common lilac is used in ornamental horticulture, planted in urban areas and grown for cut flowers. One of its most popular cultivars is white cv. Mme Florent Stepman.

Until now there have been no complete studies on developmental processes in common lilac buds and flowers during inflorescence bud formation before entering dormancy and after dormancy. The aim of our study was to observe developmental processes occurring in buds and flowers of the common lilac flowering under natural conditions in central Poland, focusing on microscopic observations of morphological and anatomical changes. After winter dormancy, the following phenological phases as described by Jedrzejuk et al. (2003) were studied: inflorescence bud swelling, inflorescence elongation, flower bud

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whitening, flower bud swelling and flowering (anthesis).

MATERIALS AND METHODS

Generative buds and flowers of common lilac cv. Mme Florent Stepman were collected every 7–10 days from July 18 to late October 2001 from shrubs grown in an ornamental plant nursery in Grodzisk Mazowiecki (Central Poland). The following year, buds were sampled between March and early May 2002, according to the following phenological phases: inflorescence bud swelling (March 11), inflorescence elongation (April 8), flower bud whitening (April 22), flower bud swelling (April 24) and flowering anthesis (April 30 to May 6). The flower pattern usually described as an exception for common lilac is the five-lobed corolla. These flowers are in the minority within the whole inflorescence of common lilac, and we did not study their morphology. The material was fixed, dehydrated and embedded in the Department of Botany of Warsaw Agricultural University. Samples were fixed for 6 h in 5% glutaraldehyde and 4% formaldehyde solution in 0.1 M sodium cacodylate buffer (pH 7.2–7.3) at 0.8 atm at room temperature. Then the samples were rinsed with the same buffer, postfixed in 2% OsO_4 in 0.1 M sodium cacodylate buffer for 2 h, and rinsed with the same buffer again. The material was then dehydrated in a graded ethanol and acetone series and embedded in hard-grade epoxy resin (SERVA) similar to Epon 812. All samples were sectioned at 2–4 μm with a rotary microtome (Jung RM2065 Supercut, Leica/Reichert-Jung). Sections were stained with 2% methylene blue and 1% Azur B at 70˚C. Observations and photographic documentation were made with a bright-field microscope (Axioskop, Opton). For SEM, the material was dehydrated in a graded ethanol series, then critical-point dried with liquid carbon dioxide, further dissected and coated with carbon. Observations and photographic documentation employed a scanning electron microscope (PHILIPS XL 30 ESEM) in the Laboratory of Electron Microscopy of Warsaw Agricultural University.

RESULTS

ANATOMY AND MORPHOLOGY OF BUD-STAGE INFLORESCENCE

Differentiation of flower primordia in the inflorescence bud was first observed in the basal part of the panicle (July 18), while only the inflorescence meristem was present in the apical part (Fig. 1). The flower primordia cells contained dense cytoplasm with easily discernible nuclei. On the first date of observations (July 18), the panicle main axis and the side branches were short, with barely visible procambial strands. On the last date of bud sampling before winter dormancy (October 22), vascular bundles with tracheary elements were observed in the main axis. The first bracts were already formed in July, with a uniseriate epidermis and 7–8 layers of mesophyll. At this time (July 18), tracheary elements and idioblasts with crystal sand were also developed in the bracts. The branches of the main axis differentiated in the axils of the bracts, acropetally. The pattern of bracts and axis branches of different orders is as follows: bract → axis branch of the first order, bract → axis branch of the second order (Figs. 1, 2).

FLOWER MORPHOLOGY

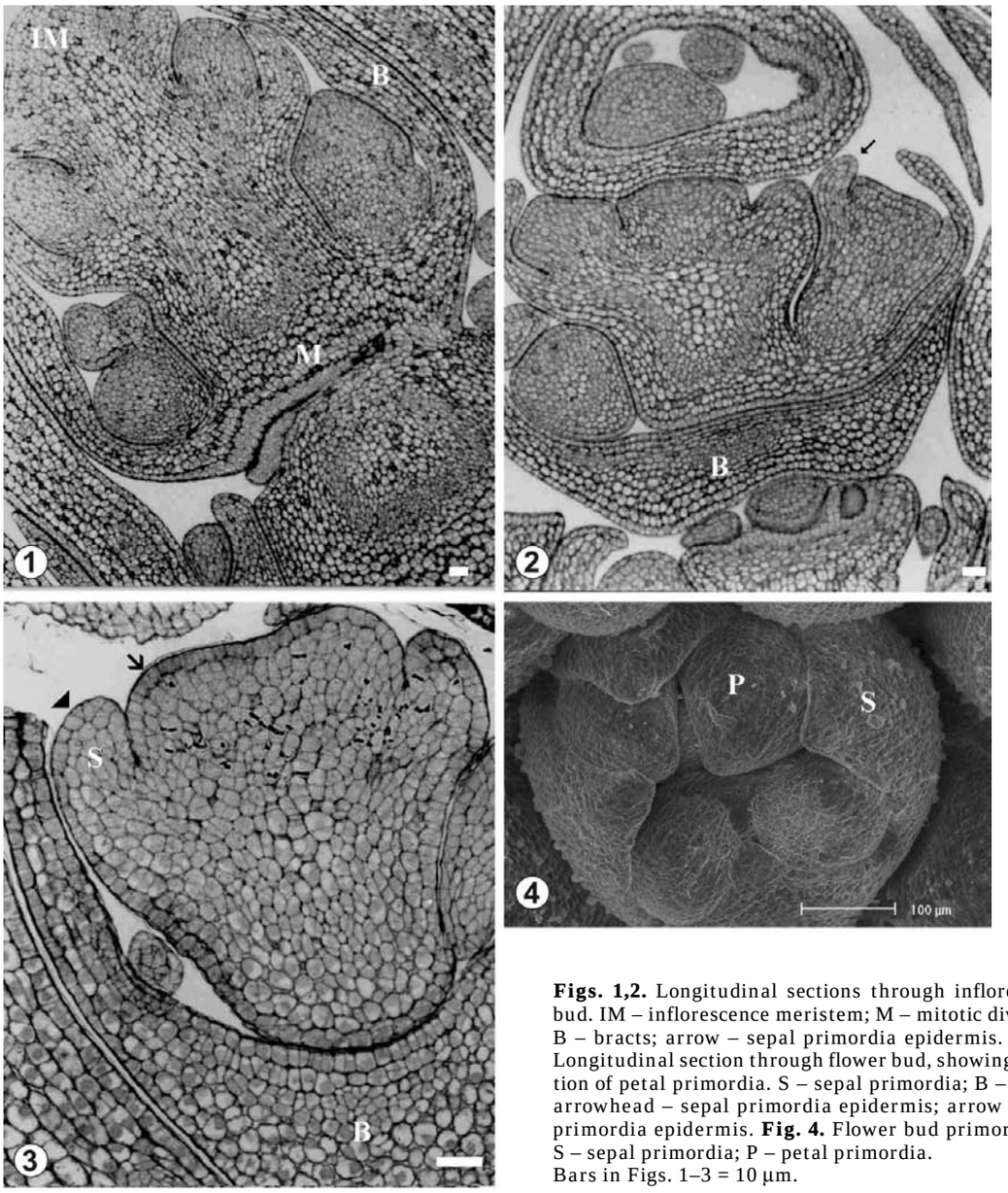
The flower of *Syringa vulgaris* conforms to the general pattern of the Oleaceae. The flower is hypogynous and perfect. The calyx is four-lobed, and the four-lobed corolla is gamopetalous with a cylindrical basal tube. Two stamens are fused with the corolla at the base. The filaments are long, and the anthers dithecal and tetrasporangiate. The anther wall comprises an epidermis, 2–3 layers of endothecium, one middle layer, and a unilayered secretory tapetum with binucleate cells. The ovary is superior and bilocular, and contains four anatropous ovules.

Calyx

Flower development began with initiation of sepals (July 18) covered by a thin uniseriate protoderm. Differentiation of sepals started at the margin of the flattened floral apex. Sepal primordia were initiated simultaneously (Fig. 2). In August, the sepal's procambial strands were discernible, and on October 22 the vascular bundles with tracheary elements were observed. When buds entered the state of winter dormancy, the sepals were covered by uniseriate protoderm with dense cytoplasm, and 4–5 layers of mesophyll cells also filled with dense cytoplasm. Numerous idioblasts with crystal sand were present from July 27. After completion of deep winter dormancy, differentiation of sepals continued and became rapid in March-April. In mid-April the spaces between mesophyll cells enlarged, and at the end of April (April 30) differentiated epidermis was visible.

Corolla

Following sepal initiation, four petal primordia initiated simultaneously at the edge of the floral meristem, alternating with sepals. Petal primordia formation started around mid-July, after sepal initiation, and produced four white petals (Fig. 3). In early petal development, frequent mitotic divisions were observed at the basal part of the petal primordium.



Figs. 1,2. Longitudinal sections through inflorescence bud. IM – inflorescence meristem; M – mitotic divisions; B – bracts; arrow – sepal primordia epidermis. **Fig. 3.** Longitudinal section through flower bud, showing initiation of petal primordia. S – sepal primordia; B – bracts; arrowhead – sepal primordia epidermis; arrow – petal primordia epidermis. **Fig. 4.** Flower bud primordia. S – sepal primordia; P – petal primordia. Bars in Figs. 1–3 = 10 µm.

Around mid-August, the basal part of the petals was narrow and contained procambial strands. At this time the petals enclosed the developing androecium and gynoecium (Fig. 4). In September the petal primordia were still covered by uniseriate protoderm cells filled with dense cytoplasm. Continuous growth of the developing hypanthium subsequently elevated the petals above the floral apex, as noted on October 2, and 5–7 layers of mesophyll tissue were present in the petals (Fig. 5). The mesophyll cells were small, with dense cytoplasm. Provascular bundles were also discernible within the mesophyll at this time. Vascular bundles with tracheary elements were present on October 22. In the next season, after completion of deep winter dormancy, differentiation of petals continued, taking a course similar to that of sepal development. The mesophyll cells enlarged and their cytoplasm lost its density. As in the sepals, the space between mesophyll cells enlarged, and completely differentiated epidermis was observed (April 30). Numerous idioblasts with crystal sand were observed in early August of the first season of observations.

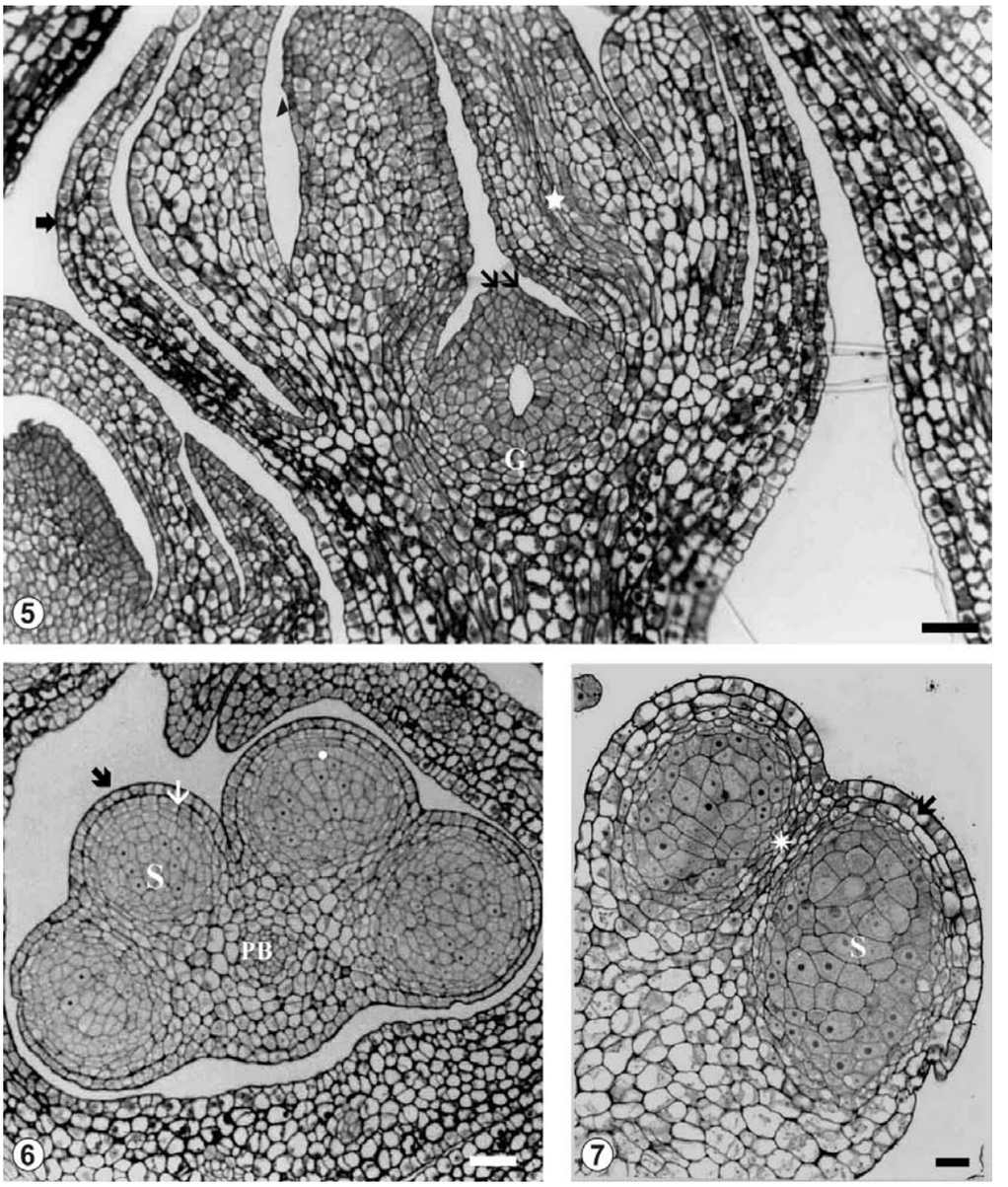
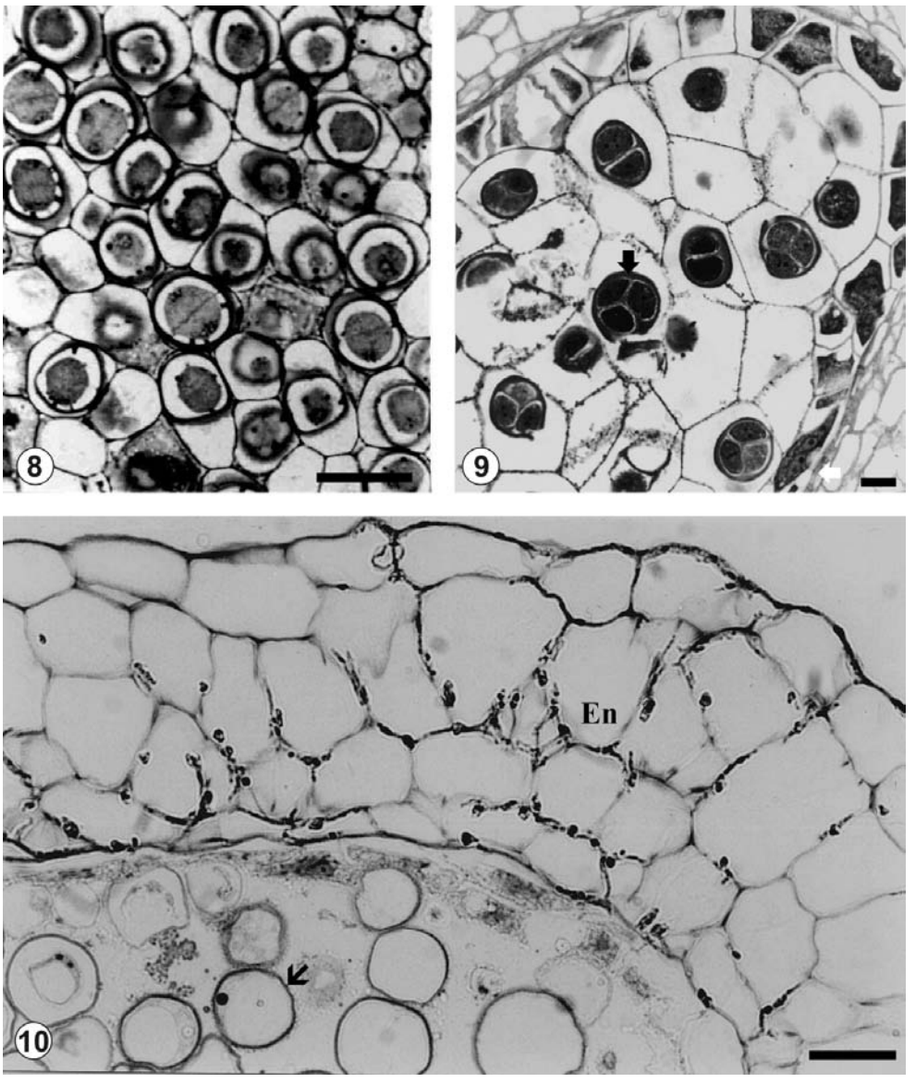


Fig. 5. Longitudinal section through flower bud. G – gynoecium; arrow – gynoecial epidermis; asterisk – procambial strand; arrowhead – petal epidermis; double arrows – sepal epidermis. **Figs. 6, 7.** Transverse section through developing anther. PB – provascular bundle; S – sporogenous tissue; black arrow – epidermis; white arrow – endothelium; white dot – middle layer; white star – septa cells. Bars = 10 μm.

Androecium

The first evidence of stamen primordia was observed at the end of July, but in most inflorescence buds the first stamen primordia were present at the beginning of August. In this period the stamens were not yet differentiated into filaments and anthers. In longitudinal section they were cylindrical, and were composed of dense-cytoplasmic meristematic cells.

In mid-August, procambial strands formed, and the stamens differentiated into anthers and filaments (Fig. 5). At the end of August, uniseriate protoderm was discernible. In September a provascular bundle formed within the connective tissue, and ~8 layers of sporogenous tissue were visible in transverse section (Fig. 6, 7). On the parietal side of the anther, anticlinal and periclinal mitotic divisions of the sporogenous cells took



Figs. 8–10. Transverse section through anther. **Fig. 8.** Pollen mother cells during meiosis (arrow). **Fig. 9.** Isobilateral microspore tetrads (arrow). **Fig. 10.** Fragment of anther wall; pollen grains visible (arrow). En – endothecium. Bars = 10 µm.

place in the first and second layers. The sporogenous cells contained dense cytoplasm. On October 22, the first pollen mother cells undergoing meiosis appeared in a few buds at the base of the inflorescence (Fig. 8, 9). Sporogenous tissue was present in most of the buds observed on that date. Also at that stage, numerous idioblasts with crystal sand were visible in the vascular bundles of the septa**.** After breaking the state of deep dormancy, the anthers continued differentiation. On March 11, sporogenous tissue differentiated into pollen mother cells in most observed buds (Fig. 8). Small, thin-walled septa cells were then visible in anthers. On April 8, meiosis or microspore tetrads were discernible in anthers. Meiotic cytokinesis was simultaneous, and afterwards the isobilateral microspore tetrads were enclosed in callose (Fig. 9). The middle layer began to degenerate at the same time. Two weeks later (April 22) the individual pollen grains separated and the tapetum became shriveled (Fig. 10). In this period the endothecium developed secondary cell wall thickenings. Changes were also visible in the stomium cells. The space between stomium cells enlarged and the cells became irregular in shape. During the following days, dehiscence occurred at the stomium (Fig. 11). The pollen grains observed on April 30 were spherical, three-colpate, bicellular, and strongly stained after fixation (Figs. 12, 13).

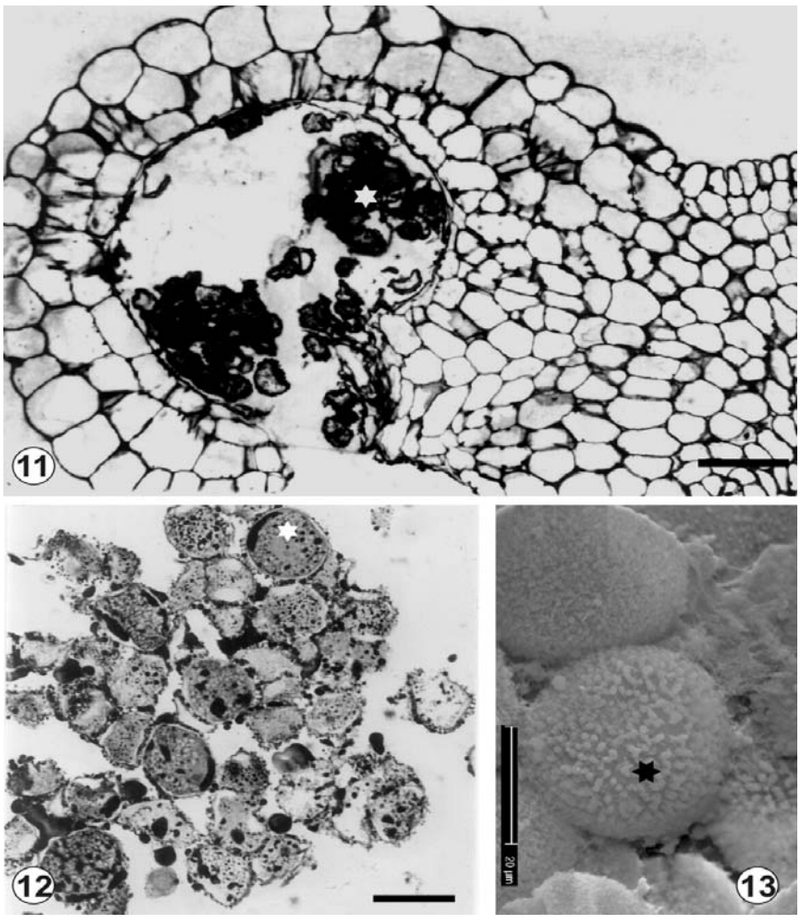
TABLE 1. Characteristic developmental features observed in anthers according to phenological phases of generative development in *S. vulgaris* L. cv. Mme Florent Stepman

	Last term before winter dormancy October 22	After winter dormancy					
		Inflorescence bud swelling March 11	Inflorescece elongation April 8	Flower bud whitening April 22	Flower bud swelling April 24	Early flowering Apil 30	Flowering anthesis May 6
Sporogenous tissue	×						
Tapetum	× (basal part of inflorescence)	×	×				
Middle layer	× (basal part of inflorescence)	×					
Middle layer shriveling			×				
Endothecium	× (basal part of inflorescence)	×	×				
Endothecium thickenings				×			
Microspore mother cells	× (basal part of inflorescence)	×					
Meiosis in microspore mother cells	× (basal part of inflorescence)		×				
Microspore tetrads			×				
Shriveled tapetum				×			
Free microspores				×	×	×	×
Anther dehiscence						×	×

The wall of mature anthers observed on April 30 and May 6 consisted of an epidermis, 2–3-layered endothecium, a single middle layer, and a uniseriate secretory tapetum composed of binucleate cells. In transverse section, the epidermal cells at the locule differed in size. In the furrow, the epidermal and the subepidermal cells were smaller than the adjacent ones, and appeared round in transverse section. These small cells probably take part in anther dehiscence. Periclinal divisions within the connective tissue were still detected in the second half of April. The filaments did not elongate until just before anthesis. Table 1 presents the most characteristic developmental features of anthers in each phenological phase.

Gynoecium

The gynoecium is the last to differentiate in the course of organogenesis. The twin carpel primordia appeared in mid-August, and were covered by thin uniseriate protoderm with isodiametric cells and dense cytoplasm. In September they elongated longitudinally and fused laterally (Fig. 5). At this stage the style began to form and the meristematic cells of the gynoecium divided. On October 22, in transverse section at the level of the ovary, two primordia of ovary septa were present, as well as the differentiating placenta. After breaking winter dormancy, the ovules developed rapidly in the ovary. The first evidence of the formation of an ovule was visible near the base of the placenta. In



Figs. 11–13. Pollen grains (asterisks). Bars = 10 µm.

transverse section, two developing ovules were visible in the ovary (Fig. 14). At this stage of ovule development, differentiating epidermis and a few layers of mitotically dividing cells were visible. Cells of the developing epidermis were filled with dense cytoplasm; vacuoles and nuclei were also observed. At the phase of inflorescence elongation, the ovule produced two subepidermal layers and subsequently the archesporial cell of the megaspores (Fig. 15). At this stage, one layer of nucellus cells and the integument was visible. A single hypodermal archesporial cell enlarged and became the megasporocyte. In early development of the ovule, the cells of the integument and nucellus were larger than those of the funiculus. In the second half of April the funiculus was observed to bend, ultimately resulting in an anatropous ovule. Mitotic divisions were still occurring in the ovule. The funiculus with a well-discernible vascular bundle was considerably elongated and formed a distinctive obturator. The micropyle was narrow and very long, located near the obturator. In the second half of April, the megasporocyte divided meiotically, producing the megaspore tetrad (Fig. 16). At the end of April the functional megaspore of the female gametophyte was visible (Fig. 17). The functional megaspore developed into a female gametophyte according to the Polygonum type. The egg apparatus consisted of an egg cell and two pear-shaped synergids.

At the end of April the nucellar cells began to degenerate. The remnants surrounded the female gametophyte, and only the endothelium was present. The integument consisted of ~10 cell layers. Periclinal divisions occurred in the integument of the mature ovule. The integument continued differentiation in late April. The inner epidermis of the integument transformed into a unilayered endothelium surrounding the female gametophyte. The elongated endothelium cells had dense cytoplasm and a centrally located nucleus. The endothelium cells were longer than the parenchyma cells of the integument.

The most important developmental features of ovule development and the critical dates are shown in

TABLE 2. Characteristic developmental features observed in ovule in phenological phases of generative development in *S. vulgaris* L. cv. Mme Florent Stepman

	Last term before winter dormancy October 22	After winter dormancy					
		Inflorescence bud swelling March 11	Inflorescence elongation April 8	Flower bud whitening April 22	Flower bud swelling April 24	Early flowering Apil 30	Flowering anthesis May 6
Ovary primordia	×						
Ovular primordia		×					
Megaspore mother cells			×				
Megaspore dyad				×			
Endothelium			×	×			
Obturator				×			
Megaspore tetrad				×	×		
Functional megaspore						×	
Mature female gametophyte							×

Table 2. The rate of ovule differentiation was slow in March and became faster in April, when about four weeks remained to completion of female gametophyte differentiation.

The stigma was yellow, wet-type and club-shaped. The receptive surface was covered with papillate epidermis (Fig. 18, 19). The style was solid. Transmitting tissue developed in the style in the beginning of April, when the papillae of the stigma differentiated. In late April the furrow of the transmitting tissue was discontinuous at the junction of the ovary. The discontinuity was probably caused by the obturator, which was growing into the transmitting tissue (Fig. 20). The discontinuity of transmitting tissue was filled at the end of April, when the cells of the obturator that grew into the style were bigger than the transmitting tissue cells (Fig. 19). The style contained two bicollateral vascular bundles extending from its junction with the ovary to the base of the stigma.

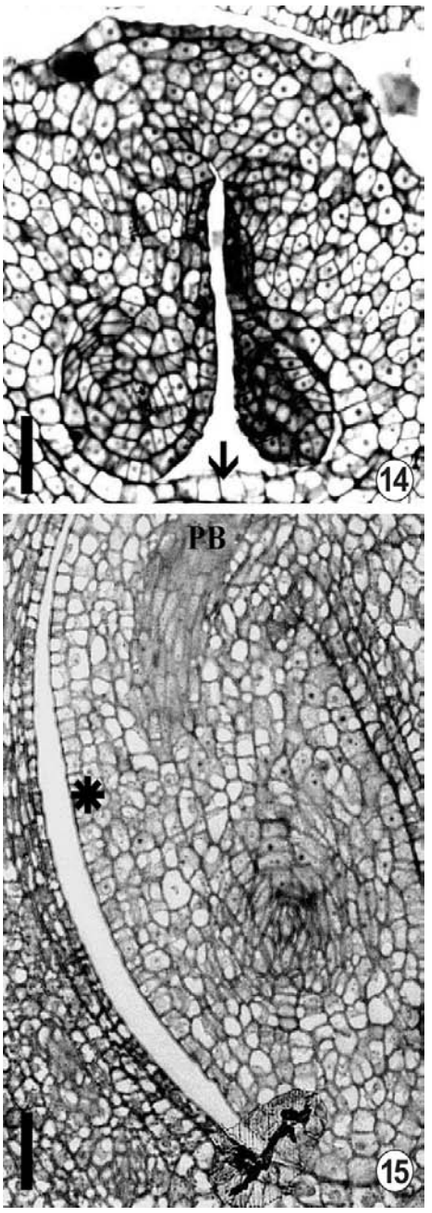
Provascular strands appeared within the gynoecium at the end of August, at first within its base. On October 22, tracheary elements differentiated in the vascular bundles at the ovary base. On April 22 of the next year, bicollateral vascular bundles were differentiated in the ovary wall and its septa, as well as in the style close to its epidermis. The epidermis cells in the mature ovary were small, with well-visible nuclei. Numerous idioblasts with crystal sand were present in the ovary wall, fewer in the septa. Similar idioblasts were also visible in the style close to its epidermis. In the mature flower, the ovary wall consisted of a uniseriate outer epidermis, ~11 mesophyll layers and a uniseriate inner epidermis. The cells of the outer epidermis were dense-cytoplasmic and bigger than the cells of the inner epidermis. Some periclinal divisions were still observed within the mesophyll.

Secretory Hairs

Secretory hairs developed in the youngest buds examined, on the epidermis of the bracts and the panicle. They consisted of two or three stalk cells and a multicellular head. At the beginning of October, secretory hairs occurred along the entire length of the sepals and on the tops of petal primordia (Fig. 21). On petal primordia the secretory hairs consisted of a single stalk cell and a multicellular head (Fig. 22), while on sepals the secretory hairs consisted of two or three stalk cells and a multicellular head (Fig. 23). No secretory hairs developed on the anthers or ovary.

DISCUSSION

The morphology of Oleaceae was studied by Bugała (1979), and some aspects of generative organ anatomy (e.g., anthers, pollen grains, nucellus, female gametophyte structure) were investigated by Ander-



Figs. 14, 15. Longitudinal sections through developing ovules. arrows – ovary epidermis; asterisk – integument epidermis; PB – provascular bundle. Bars = 10 µm.

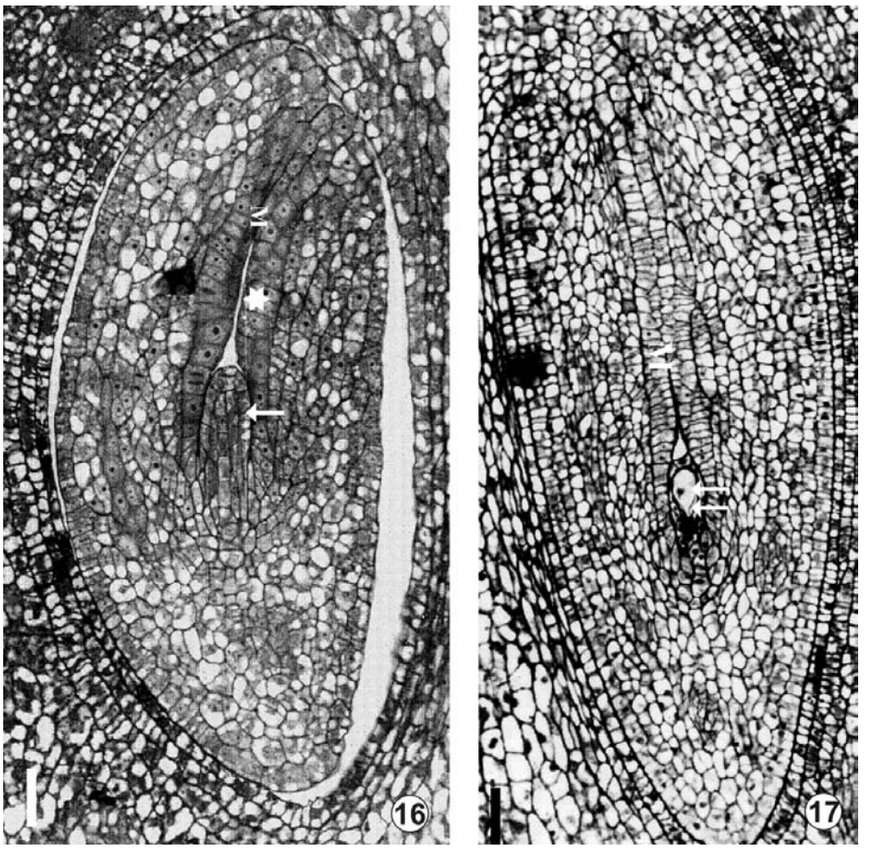
son (1931), King (1938), Copeland (1960), Mahesvari Devi (1975), Bhargava (1980) and Johri et al. (1992). In our work we focused on the development of the entire flower bud in a commercial cultivar of common lilac. We observed anatomical and morphological changes in developing buds and flowers of cv. Mme Florent Stepman before and after dormancy. When the buds resumed growth in the spring, we focused on events occurring in the bud and described flower anatomy in the phenological phases given in Material and Methods. The purpose was to observe flower differentiation during the whole developmental cycle in common lilac.

Our observations revealed the close similarity of flower bud development between common lilac and other members of Oleaceae (Esau, 1973; Bugała, 1979; Johri et al., 1992). In the cultivar Mme Florent Stepman, the morphological features of the flower whorls were similar to those described for the family (Bugała, 1979, Johri et al., 1992). In common lilac the organogenetic order of formation of an individual flower was strictly acropetal, like that of other trees such as *Juglans regia* (Polito and Pinney, 1997), *Malus domestica* (Huang, 1996), *Amelanchier alnifolia* (Steeves et al., 1991), *Oemleria cerasiformis* and *Exochorda racemosa* (Evans et al., 1999).

Studies on Rosaceae (Evans et al., 1999) showed two patterns of flower initiation within an inflorescence. The floral primordia are initiated in the axil of spirally arranged bracts, as for example in *Oemleria cerasiformis*, *Exochorda racemosa* and *Amelanchier alnifolia*; the flowers are also arranged acropetally. In *Syringa vulgaris*, the development of both inflorescence and flower is acropetal, as in *Oemleria cerasiformis*, *Exochorda racemosa* and *Amelanchier alnifolia*. In lilac, as in the plants mentioned above, the bracteoles differentiate before the adjacent flower primordia differentiate. The difference is that axis branches of different orders occur in common lilac. In the genera mentioned above, flower primordia differentiate in the bract axils. Petal primordia appear soon after sepal primordia initiation. In lilac, in an early stage of flower bud development the petal primordia fold, enclosing the androecium and gynoecium. Similar folding was described in Rosaceae by Evans et al. (1999).

The stamen primordia in lilac and in *Amelanchier alnifolia* develop similarly (Steeves et al., 1991). By the onset of winter dormancy, the stamens differentiate into anthers and filaments, and the anthers contain microsporocytes and the tapetum. In this aspect, *S. vulgaris* differs from *Amelanchier alnifolia* (Steeves et al., 1991), since the tapetum and pollen mother cells appeared in April after breaking winter dormancy.

The timing of flower organ appearance and development generally was close to that reported by Steeves et al. (1991) in *Amelanchier alnifolia* flowers. In lilac the stamens appeared soon after the petal primordia, and the anatomy of the anther was similar to that of other Oleaceae. The anther wall comprises a uniseriate epidermis, 2–3-layered endothecium, single middle layer and secretory tapetum, as in *Jasminum calophyllum* (Johri et al., 1992). The tapetum is irregularly biseriate in *Fraxinus velutina* and *Jasminum pubescens*, and the tapetal cells are multinucleate (Copeland, 1980; Bhargava, 1980; Johri, 1992). In lilac anthers, two layers of binucleate tapetum develop.



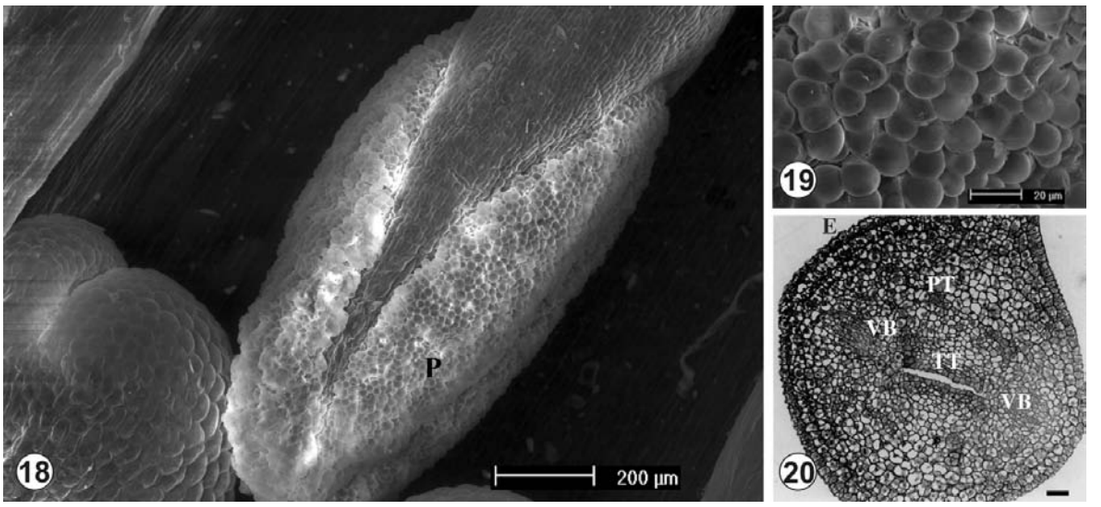
Figs. 16,17. Longitudinal sections through developing ovules. asterisk – endothelium; arrow – megaspore tetrad; double arrows – central cell vacuole; M – micropyle. Bars = 10 μm.

The tapetal cells persist for a long time and begin to shrivel when the pollen grains develop. This observation confirms the secretory type of lilac tapetum reported by Johri et al. (1992). The microspore tetrads are isobilateral; the pollen grains are two-celled and three-colpate, in accordance with earlier data on lilac by Johri et al. (1992), who also described three-celled grains in *Jasminum calophyllum*. When the pollen grains mature, the septum dehisces at the apex of the anthers exclusively, similarly to anther dehiscence in Solanaceae (Rodriguez, 2000).

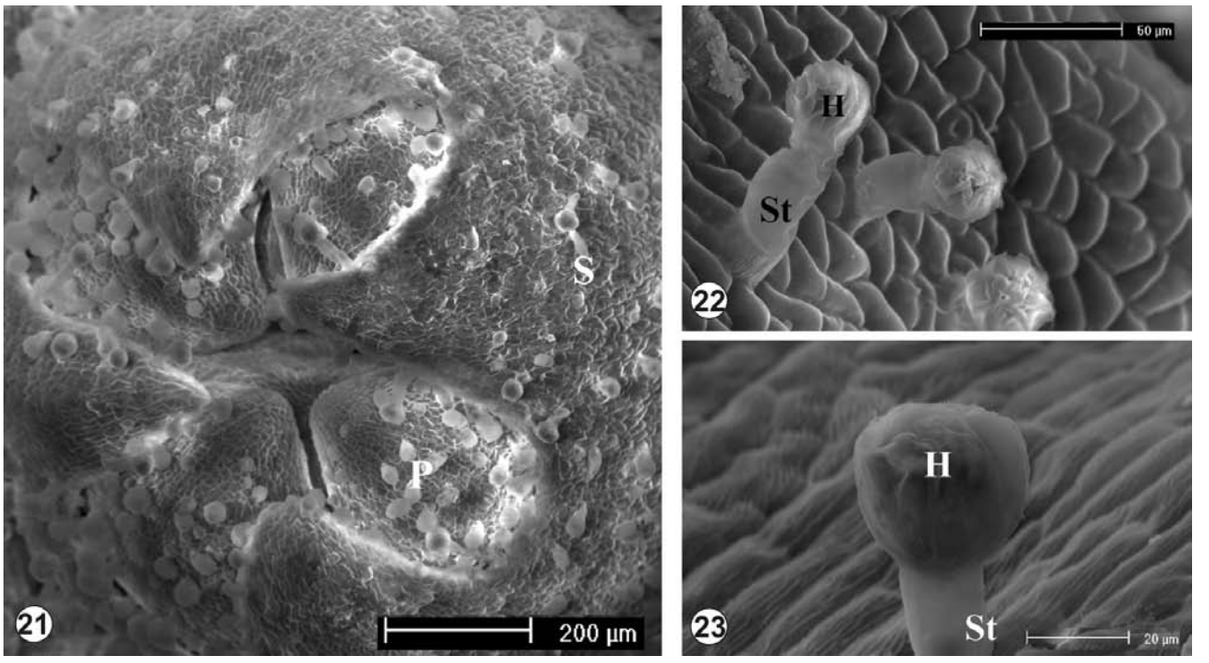
In *Syringa vulgaris* L. the stigma is club-shaped and of wet type, like most members of Solanaceae (Rodriguez, 2000; Kopcińska et al., 2002). To the best of our knowledge, there are no literature reports on stigma type in other Oleaceae plants. The stigma of lilac is yellow and covered by papillate stigmatoid epidermis, and the style is long, solid and white. Differentiation of the stigma begins in early April and is completed in late April.

The ovary is two-carpellate in *Syringa* spp. as in *Forsythia* spp., in agreement with observations made by Bugała (1979). The style is solid, and differentiated from two carpels. The ovary is bilocular with two ovules in every locule. The ovary wall consists of an outer and inner epidermis with mesophyll parenchyma interposed. In the mature flower, mesophyll cells still divided mitotically as in *Solanum muricatum* (Kopcińska et al., 2002). The septa of the ovary is perpendicular to the anthers. As in *Amelanchier alnifolia* studied by Steeves et al. (1991), the ovule of lilac is formed in early spring. The female gametophyte structures are differentiated in April. At this time the archesporial cell of the megaspores is present. The female gametophyte differentiates into an egg cell, two synergids, a central cell and three antipodals, as in most angiosperms (Anderson, 1931; King, 1938; Johri, 1992; Owens and Sornsathapornkul, 1999; Anisimova et al., 2000). The lilac ovule is anatropous, unitegmic and tenuinucellate, like that of *Jasminum sp.* (Johri et al., 1992). At maturity the inner epidermis of the integument forms a unilayered endothelium that surrounds the female gametophyte. Anisimova et al. (2000) described a similar endothelium in *Vaccinium myrtillus*.

According to Johri et al. (1992), an endothelium differentiates in some species of Oleaceae. Maheswari



Figs. 18–19. Stigma covered by papillate epidermis. **Fig. 20.** Transverse section through style. P – papillae. VB – vascular bundle; TT – transmitting tissue; PT – parenchymatic tissue; E – epidermis. Bar = 10 µm.



Figs. 21–23. Secretory hairs. S – sepals; P – petals; H – secretory hair head; St – secretory hair stalk.

Devi (1975) found it in *Jasminum* sp., where it covered only the lower half of the female gametophyte. In lilac the endothelium surrounds the whole female gametophyte, and the endothelial cells are longer than the parenchymatic cells of the integument. The micropyle is long, like that of *Vaccinum myrtillus* L. (Anisimova et al., 2000), and located near the obturator, as in *Prunus persica* (Reinoso et al., 2002). No reports regarding micropyle and obturator length were found for other Oleaceae. The tetrad of megaspores is linear. The chalazal megaspore develops into the female gametophyte according to the Polygonum type, similarly to *Syringa villosa* (Johri et al., 1992), Rosaceae (Johri et al., 1992; Reinoso et al., 2002), Commelinaceae (Hardy

et al., 2000), and Ericaceae (Anisimova et al., 2000). It is not obligatory in Oleaceae plants; in *Olea chrysophylla* and *Olea europaea*, development of the female gametophyte is bisporic (Anderson 1931, King 1938). Multiple female gametophytes were observed in *Jasminum* (Maheswari Devi, 1975).

In April the rate of development of the lilac ovule and anthers increases. Similar phenomena were observed in the flower primordia of other trees including *Amelanchier alnifolia*, *Oemleria cerasiformis*, *Exochorda racemosa* (Steeves et al., 1991) and *Prunus persica* (Reinoso et al., 2002). Reinoso et al. (2002) called this the 'rapid maturation phase,' characterized by an increase in cell enlargement, differentiation and specialization of all bud tissues.

Our study showed that flower bud development in common lilac lasts two vegetative seasons, as in other trees. The development of flower primordia within the inflorescence starts at approximately the same time. Studies carried out on *Amelanchier alnifolia* (Steeves et al., 1991) and *Prunus persica* (Reinoso, 2002) showed considerable similarity in the timing of events in the differentiation of flower primordia in these genera and *S. vulgaris*.

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