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RESEARCH ARTICLE

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# Initiation and development of resin ducts in the major organs of *Pinus massoniana*



**Abstract** The structure, distribution and patterns of resin ducts in processes of its initiation and development were studied with the methods of thin section and ultrathin section. This paper emphasized the ultrastructural changes during canal development by a ring of the live epithelial cells, and the epithelial cells were usually surrounded with one or two layered sheath cells, which were normal parenchyma cells in some primary resin ducts and became dead cells with thick walls in other primary and secondary resin ducts. The resin ducts were found to occur in almost all organs, except in cotyledon. The resin ducts were formed by schizogeny and their development can be divided into three stages (e.g., initial stage, formation stage and mature stage). At the initial stage, the initial cells had many plastids without integral membrane structures, which contain one or two starch grains in them, and there are a few black osmiophilic droplets on the endoplasmic reticulum and membranes. A small number of osmiophilic droplets were present in the plastids. At the formation stage, the number of plastids, mitochondria and Golgi bodies in epithelial cells increased. The plastids were commonly surrounded by endoplasmic reticulum sheath. The larger osmiophilic droplets in cytoplasm and the smaller osmiophilic droplets on the plastids envelope, mitochondrion envelope and Golgi vesicles obviously increased in number during canal developing. At the mature stage, the cytoplasm of epithelial cells became thin with small nucleus. The number of mitochondria and Golgi body decreased, but numerous plastids still existed. Osmiophilic droplets were abundant in epithelial cells as in previous status. Taken together, the structures of plastids in epithelial cells gradually became well developed and the synthesis of resin was remarkably enhanced during resin duct formation and plastids should be the main site for resin synthesis.

**Keywords** *Pinus massoniana*, resin ducts, development, ultrastructure

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## 1 Introduction

*Pinus massoniana* is an indigenous tree species to China, which is extensively distributed in 17 provinces south of Qinling-Huaihe and east of Yunnan-Guizhou Plateau (Zhou, 2001). Since 4 indexes, including MOR, MOE, longitudinal compressive stress, and hardness of end-face, of *P. massoniana* are higher than those of *Cunninghamia lanceolata* or *Pinus koraiensis* (Wu, 1963), it is widely used in architecture, mine timber, sleepers and bridges. Especially with the rise and development of the industry on fiber, wood shaving and plywood, *P. massoniana* timber, even its branches, and small-diameter thinnings have become the primary raw materials of wood-based panel industry. *P. massoniana* is a good material for making paper because of its high content of cellulose and long tracheids. It is also the main oleoresin-tapping tree species and the most important forest tree species as well (Zhao et al., 2007). With its very high economic value, *P. massoniana* takes half of the forests in south of China (Sun et al., 2007).

Resin duct is a common self-protective structure among Pinaceae. It is the first defense from insects and pathogens (Berryman, 1972; Boucher et al., 2001). Resin secreted by resin ducts is a mix of terpenes, which is transparent and colorless. The two components of resin are turpentine and colophony (Phillips et al., 1999). As a result, distilled resin can be turned into turpentine and colophony, which are key industry raw materials. China is the biggest resin-producing country in the world and the biggest resin-exporting country

(Song, 2002). There are over 20 kinds of pine trees for resin tapping, but 90% of the resin comes from *P. massoniana*. Quite a lot of people have made effort on the basic research of *P. massoniana*, especially the geographic variation (National Cooperative Group of *Pinus massoniana* Provenance Tests, 1986; Qin et al., 1990; Yue et al., 1994), chromosome analysis (Fang et al., 1983, 1990; Chen et al., 1985; Xu et al., 1998, 2001) and nutrient cycles of planted forests (Ma, 1988; Xiang et al., 2002; Mo et al., 2002). However, few people have studied the resin ducts of *P. massoniana*. Only the initiation and development of resin ducts in stems have been studied (Geng, 2000; Li et al., 2004). This paper studied the initiation and development of resin ducts in the major organs of *P. massoniana* in order to find out the structure, distribution and developing path and then to learn about the sites of resin synthesis, transportation and secretion, which can provide a theory basis for rational resin tapping, raising the yield and quality of resin, and further exploitation and utility of resin plants.

## 2 Materials and methods

### 2.1 Materials

Twenty-year-old *P. massoniana* planted in South China Agricultural University and seedlings germinated from their seeds.

### 2.2 Methods

#### 2.2.1 Thin section

We chose the shoot apex of *P. massoniana*, cambium layer of newborn branches, needles, cotyledons, roots and hypocotyls of seedlings. They were processed as follows: cut into 1 $mm^3$, double-fixed by glutaraldehyde (4%) and osmic acid (1%), dehydrated by ethanol (a set of consistency), filtered with propylene oxide, Epon812 embedded, turned into thin sections of 1–2 μm by Austria Jung ultra-microtome and dyed in PAS/TBO (Xu et al., 1986). We observed the morpha and development of resin ducts under Leica DMLB microscope and took photos.

#### 2.2.2 Ultrathin section

Samples went through the same process with thin section. After Epon812 embedding, we made them into ultrathin sections of 70–90 nm by Leica UCT microtome. Then we dyed the sections in uranyl acetate and lead citrate. We observed them with Philip FEI-TECHNAI 12 transmission electron microscope and took photos.

## 3 Results and analysis

Continuous sections have shown that resin ducts occur in almost all organs, except in cotyledon of *P. massoniana*. The structure, initiation and development of resin ducts were almost the same as well. Table 1 shows the characteristics of the cross-section of resin ducts in *P. massoniana*.

### 3.1 Resin ducts in the stem

#### 3.1.1 Primary resin ducts

Based on the observation of the continuous transversal sections of *P. massoniana* stem tip, we can conclude that differentiation of protoderm, procambium and ground meristem begins at 200 μm away from the growing point. Cells of procambium are small, which are dark-dyed and have thick protoplasm, and exist in bundles in the ground meristem. At 340 μm away from the growing point, in the ground meristem on either side of each procambium bundle, there is a rosette cell cluster composed by 4 to 6 cells, the size of which is similar to that of cells in ground meristem, but the nucleus of which are bigger and dyed darker (Fig. 1a), as a good way to tell from other cells. These are initial cells of resin ducts in the cortex. At 450 μm away from the growing point, the cell walls, which are in the center of the rosette initial cell cluster in the cortex, begin to expand and dissolve, even with cracks appearing (Fig. 1b). Meanwhile, further mitosis of initial cells makes the "rosette" figure more obvious. Later intercellular space extends along cell walls and expands to irregular space surrounded by 4 to 5 cells (Fig. 1c), which will develop into epithelial cells. Moreover, the 1 or 2

**Table 1** The characteristics of the cross-section of resin ducts in *P. massoniana*

| | stem | | root | hypocotyl | needle |
|---|---|---|---|---|---|
| | primary resin duct | secondary resin duct | | | |
| number of initial cells | 4–6 | 4 | 4–6 | 4–6 | 4–6 |
| diameter of duct/μm | 190–240 (cortex) | 35–40 | 20–26 | 12–15 | 45–61 (mesophyll) |
| | 9–12 (vascular bundle) | | | | 11–14 (vascular bundle) |
| number of epithelial cells | 10–20 | 6–14 | 6–14 | 6–10 | 6–12 |
| number of layers of sheath cells | 1–2 | 1 | 1–2 | 1–2 | 1 |
| formation mode of resin duct | schizogeny | schizogeny | schizogeny | schizogeny | schizogeny |

Note: Measuring 20 resin ducts in each organ, respectively.

layers of cells surrounding epithelial cells will be the sheath cells in the future. With the further enlargement of the duct, radial cell walls of some neighboring epithelial cells also split up. From the gap, a few sheath cells insert into the epithelial cells and then become a component of the epithelial cells, which will add to the number of the epithelial cells. At the same time, the epithelial cells adjust themselves to the enlargement of duct by tangential extension and anticlinal division. When the duct is circled by 9 to 10 epithelial cells and its transection is oval, the epithelial cells gradually tangential extend, and the volume of which is smaller than the sheath cells (Fig. 1e). The number of the epithelial cells is getting bigger and bigger with the development of resin ducts. In a mature resin duct, on average, there are 10 to 20 epithelial cells. Most of them are tangentially extending-like, with thin cytoplasm, small nucleus and an obvious large central vacuole (Fig. 1d,f). At this moment, a lot of polyphenol accumulates in the sheath cells. With the development of cortex, resin ducts are finally destroyed by cortex. In the primary vascular tissue, resin ducts only exist in the primary xylem. Each vascular bundle has a resin duct. Resin ducts in the primary xylem originate from the procambium, which has the same developing path with cortex resin duct (Fig. 1g,h). When the heartwood forms, epithelial cells of primary xylem expand into tylosoids to plug up the resin duct.

#### 3.1.2 Secondary resin ducts

The secondary resin ducts can be divided into two types, longitudinal and radial (Fig. 1k). Longitudinal resin ducts are distributed in the secondary xylem. On the growing stem transection, there are four-cell cluster among the cells formed by spindle initial cells of vascular cambium layer (Fig. 1i). These cells are in big volume and have thick protoplasm, with distinct nucleus in them, which make them very different from other cells nearby. They are called initial cells of longitudinal resin ducts. The middle layer where the four cells connect expands and dissolves and then intercellular space emerges. The intercellular space gets bigger during development. The cells around it become epithelial cells. Through periclinal and anticlinal division, more epithelial cells will be existed to get used to the enlargement of resin ducts. During the enlargement, it can be seen that sheath cells insert into two adjacent epithelial cells in order to fit themselves into the latter. When the intercellular space of resin duct enlarges to almost an oval shape, sheath cells around epithelial cells have already differentiated clearly (Fig. 1j). As the development of a resin duct is finished, it is similar round, with periclinally extended epithelial cells and thicker sheath cell walls. Protoplasm of some cells disappeared and the inner layer of their cell walls suberification (Fig. 1i). Meanwhile, tracheids around the resin duct have differentiated completely. When the heartwood of secondary xylem forms, epithelial cells will expand into quasi-tylosis to plug up the resin duct. Radial resin ducts are distributed in the rays of secondary xylem and phloem, connecting with each other through vascular cambium and longitudinal resin ducts (Fig. 1k), so that a 3D reticular system of resin ducts is generated in secondary xylem of stems.

### 3.2 Resin ducts in roots

There is a mass of dark-dyed cells in close order just close to the vessel of primary xylem in roots, which are initial cells of resin ducts in roots (Fig. 1l). During the development, intercellular space forms in the middle of four initial cells. With the intercellular space getting bigger, the four initial cells become epithelial cells, and through periclinal division, more sheath cells are formed by epithelial cells, while through anticlinal division and insert growth of sheath cells more epithelial cells are generated to get used to the enlargement of the resin duct. Epithelial cells gradually tangentially extend with the development. Similar round-shaped lumen on the transaction is the sign of a mature resin duct (Fig. 2a). At this moment, epithelial and sheath cells are still parenchyma cells.

### 3.3 Resin ducts in hypocotyl

Between the two adjacent vascular bundles in hypocotyl, there are usually four to six dark-dyed cells aligned in close order with dense protoplasm, which differentiate them from others easily. These cells are called initial cells of resin ducts (Fig. 2b). Intercellular space emerges among initial cells (Fig. 2c). With the intercellular space getting bigger, through periclinal division, the initial cells form sheath cells, while through anticlinal division and insert growth of sheath cells more epithelial cells are generated to get used to the enlargement of the resin duct. There are 6 to 10 epithelial cells in a mature resin duct (Fig. 2d).

### 3.4 Resin ducts in needles

At the beginning of the initiation of leaf primordia on the branch apex, initial cells of resin ducts do not exist yet. When the length of needles reaches 2 to 3 mm, a few rosette structures emerge under the needle surface. Usually, there are 4 to 6 cells in a rosette structure, which are small, dark-dyed, in close order and with dense cytoplasm, called initial cells of resin ducts (Fig. 2e). With the development of the initial cells of resin ducts, the middle layers of the cell walls of two adjacent cells centered in the initial cells dissolve and intercellular space forms (Fig. 2f). Then the intercellular space gets bigger and grows into a duct encompassed by four cells, which are going to be the epithelial cells of the future resin ducts. Cells on one or two layers beyond the four cells are developing into sheath cells. More epithelial cells come out through anticlinal

division and make the resin duct bigger. When the length of needles reaches 5 cm, the differentiation of resin ducts in mesophyll tissue is almost done. Epithelial cells tangentially extend and have thin cell walls, while the cell walls of sheath cells get thicker (Fig. 2g). At this moment, protocambium is still differentiating on, and rosette cell clusters are found in primary xylem, which are called initial cells of resin ducts in leaf veins. They also develop into resin ducts of primary xylem in needles in the same way as above mentioned (Fig. 2h). In the late stage of needle development, epithelial cells of resin ducts usually expand into tylosoids to plug up the resin duct in needle veins.

### 3.5 Ultrastructural changes in the development of resin ducts in stem cortex

A set of changes takes place about the morphology and structure of the cells during the development of resin ducts in stem cortex. Based on the morphological changes of the cells, the development of resin ducts can be divided into three stages (e.g., initial stage, formation stage and mature stage). Ultrastructural changes also happen in epithelial cells of resin ducts.

#### 3.5.1 Initial stage

Initial cells of resin ducts in stem cortex are usually aligned in rosettes of 4 to 6 cells. There is dense cytoplasm, many plastids (Fig. 2i), small vacuoles and big core in an initial cell. The plastids are oval and a little big, distributed uniformly in cytoplasm. Often 1 or 2 starch granules are in the plastid with no membrane structures in them (Fig. 2j). Endoplasmic reticulum can be found near some plastids (Fig. 2j). On the endoplasmic reticulum and membranes, there are a few black osmiophilic droplets (Fig. 2j).

#### 3.5.2 Formation stage

The middle layer of cell walls between the rosette initial cells expands and forms intercellular space. The intercellular space extends along two sides of cell walls and a duct encompassed by 4 to 6 cells forms. These cells are developing into epithelial cells of resin ducts, in which more plastids form. When the resin duct is encompassed by 6 to 10 epithelial cells, there will be plenty of mitochondria, Golgi bodies, endoplasmic reticulums and plastids with large starch granules inside. Sheath of endoplasmic reticulums is obvious. Big black osmiophilic droplets can be seen on the outer membrane of plastids and Golgi bodies (Fig. 2k).

#### 3.5.3 Mature stage

A resin duct is made up of 10 to 20 epithelial cells with 1 or 2 layers of sheath cells outside. There is weak cytoplasm and a big vacuole in an epithelial cell. The core is small, accompanied with less mitochondria and Golgi bodies but still with many plastids. There is no starch granule in most plastids, which is enclosed by an ER sheath (Fig. 2l). Large gray osmiophilic droplets can be seen on the core membrane, surrounded by ER connected to plastid sheath (Fig. 2l). Normally, ER with osmiophilic droplets on it is close to plastid membrane and connects to it (Fig. 2l). Plastids and ER sheath are close to plastid membrane as well. Moreover, there are osmiophilic droplets on both sides of a plastid membrane. A vesicular structure can be found near an osmiophilic droplet. Near those plastid membranes going through osmiophilic droplets are also some small vesicles. Some osmiophilic droplets are enveloped by sunk plastid membranes.

## 4 Conclusions and discussion

The resin ducts were found to occur in almost all organs of *P. massoniana*, except in cotyledon. The resin ducts are relatively large intercellular spaces surrounded by a layer of parenchyma cells, and the epithelial cells are usually surrounded with one or two layered sheath cells. Resin ducts in stem are distributed in the cortex and in primary and secondary vascular systems. Resin ducts in roots are distributed in primary and secondary vascular systems. Resin ducts in needles are distributed in mesophyll tissue and primary vascular system.

Formation of secretory passage can be divided into three types: schizogeny, lysigeny and schizo-lysigeny. The middle layer of cell walls of *P. tabulaeformis* dissolves so that cells depart from each other, which is schizogeny. Lysigeny is the result of some cells breaking down. Esau (1965) and Fahn (1979) thought resin ducts of conifers were formed by schizogeny. Wu (1990) found that in roots, stem and all kinds of sexual organs of *P. sinensis*, primary and secondary resin ducts were formed by schizogeny, while resin ducts in nucellus tissue of ovule were formed by lysigeny. Li et al. (2004) have proven the hypothesis by cell chemical method that resin ducts in stem cortex of *P. massoniana* were formed by schizogeny. Our observation revealed that resin ducts in roots, stems and leaves of *P. massoniana* were all formed by schizogeny. We did not manage to observe the development of resin ducts of *P. massoniana* in nucellus tissue for some reason, so we are not able to give a conclusion whether or not there was only one way of generation like *P. sinensis*.

The development of resin ducts in the roots, stems and leaves of *P. massoniana* is almost the same. According to the changes of cell structure, we can divide the development of a resin duct into three stages, namely initial stage, formation stage and mature stage. In different organs, resin ducts develop a little differently, especially in initial stage. Generally speaking, primary resin duct in roots, stems and leaves are made of 4 to 6 initial cells on average aligned in

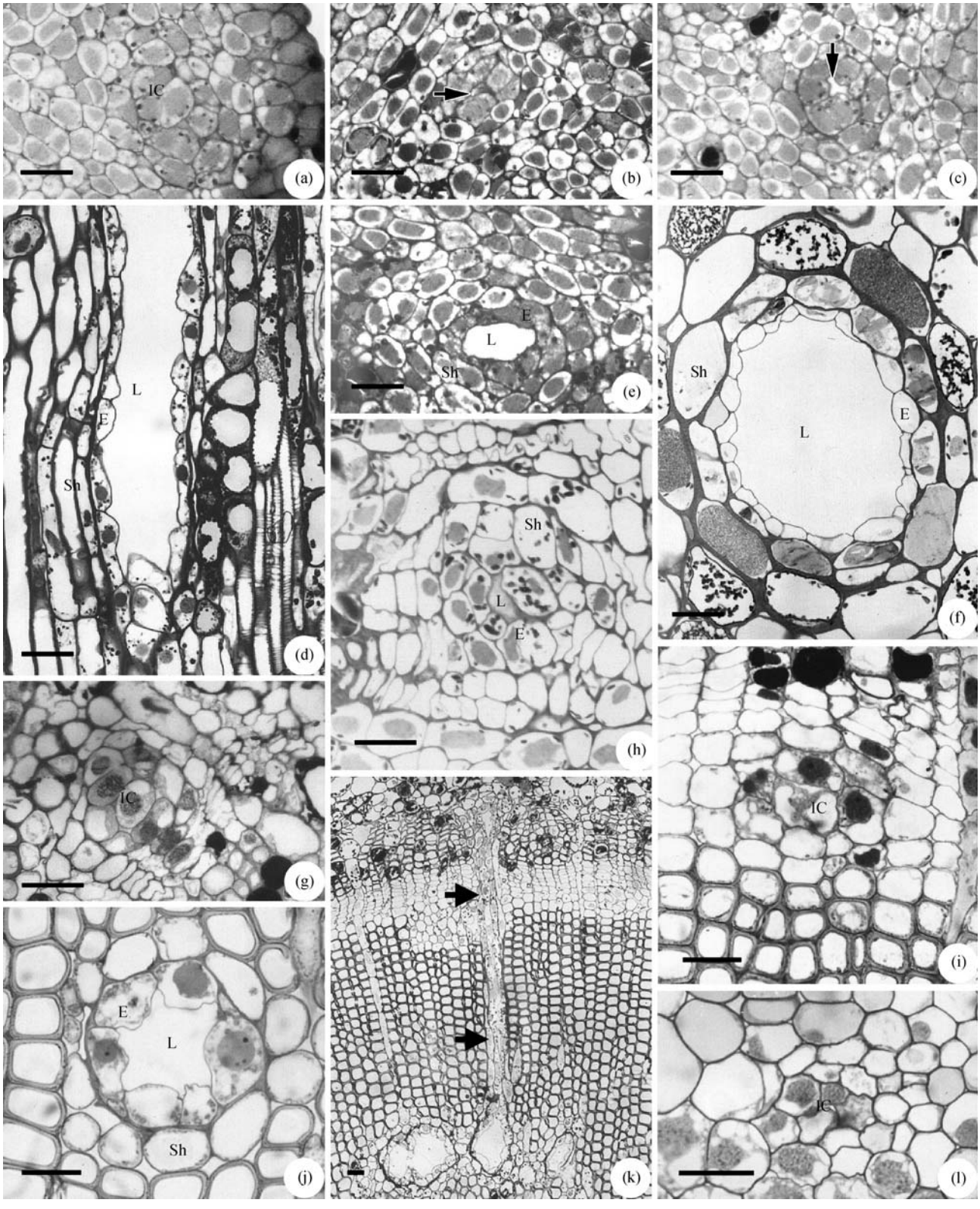


**Fig. 1** Initiation and development of resin ducts in the major organs of *P. massoniana*. Except Fig. 1(d), the rest are cross-sections of resin ducts. (a) The initial cells of cortical resin duct; (b) The intercellular space appeared in the corner among the initial cells (arrow); (c) The intercellular space enlarged (arrow); (d) Mature resin duct in longitudinal section; (e) The resin duct lumen formation; (f) Mature cortical resin duct; (g) The initial cell of resin duct in primary vascular bundle; (h) Mature resin duct in primary vascular bundle; (i) The initial cell of secondary resin duct in stem; (j) Mature secondary resin duct in stem; (k) The vertical resin ducts connect with horizontal resin duct (arrows) in stem; (l) The initial cell of primary resin duct in root. bar = 50 μm in (a)–(g), 20 μm in (h)–(i), 25 μm in (j)–(l). IC: initial cell; E: epithelial cell; L: lumen; Sh: sheath cell.

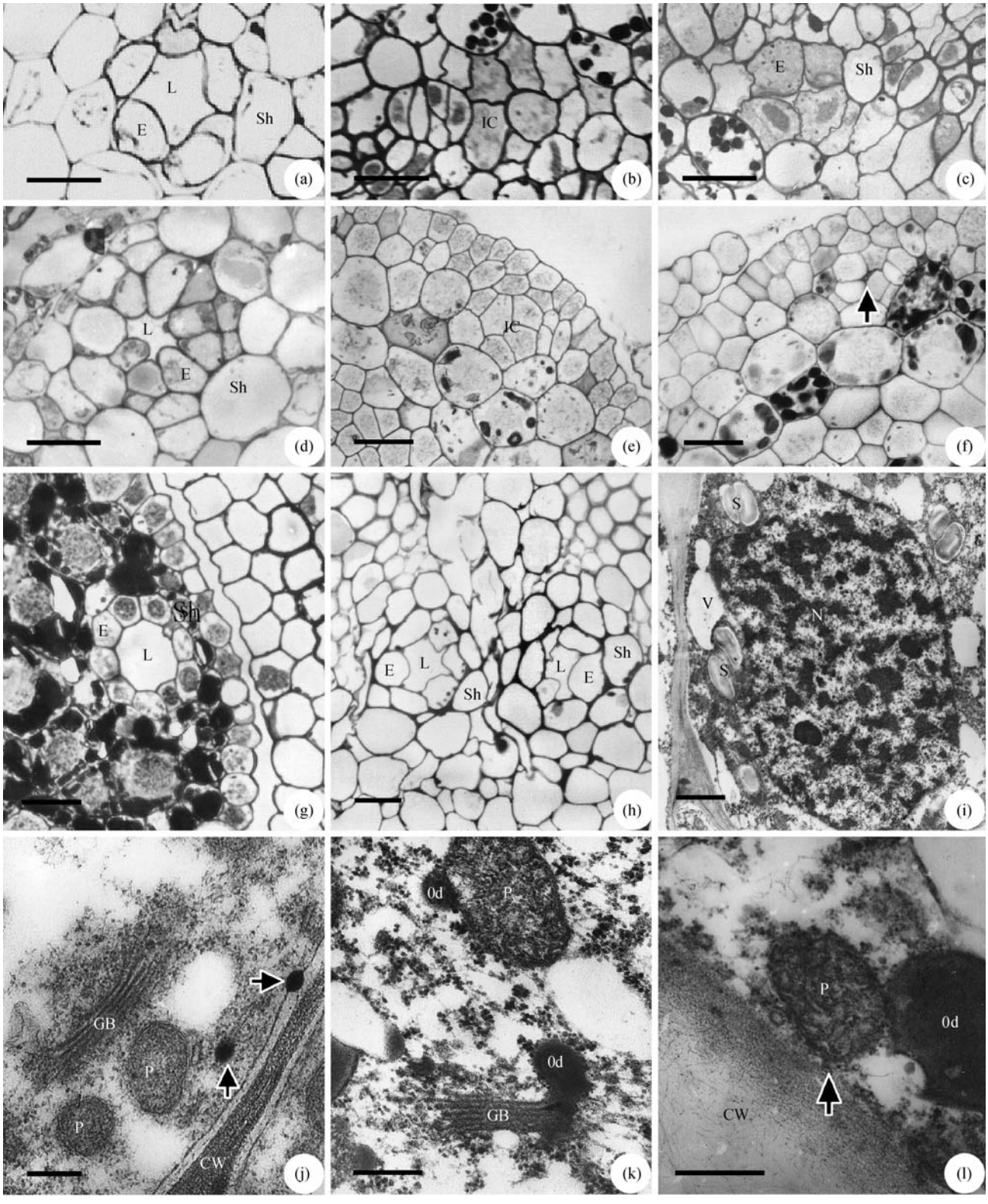


**Fig. 2** Initiation and development of resin ducts in the major organs of *P. massoniana*. (a)–(h) Cross-sections of resin ducts. (a) Mature resin duct in roots; (b) The initial cell of resin duct in hypocotyl; (c) The resin duct lumen formation in hypocotyl; (d) Mature resin duct in hypocotyl; (e) The initial cell of resin duct in needle; (f) The lumen formation in needle; (g) Mature resin duct in needle; (h) Mature resin ducts in vascular bundle of needle; (i)–(l) TEM of cortical resin duct in stem; (i) The initial cell of resin duct, showing small vacuoles and starch grains; (j) The initial cell, showing osmiophilic droplets (arrow) in plasmalemma (arrow) and osmiophilic droplet. bar = 25 μm in (a)–(d), 20 μm in (e)–(h), 2 μm in (i), 500 nm in (j)–(l). IC: initial cell; E: epithelial cell; L: lumen; Sh: sheath cell; CW: cell wall; GB: Golgi body; N: nucleus; Od: osmiophilic droplet; P: plastid; S: starch grain; V: vacuole.

rosettes. However, there are usually four initial cells in the resin ducts of secondary xylem in stems, not aligned in rosettes. It is the diverse origins of initial cells of resin ducts and difference of cell division direction that lead to this phenomenon. Primary resin ducts originate from ground meristem or protocambium, which have diverse directions and can form rosette cell clusters. Resin ducts in secondary xylem are formed by daughter cells from chordwise division of spindle initial cells in vascular cambium so that they cannot form rosette shape.

Changes of epithelial cells ultrastructure during the development of resin ducts observed by electron microscope have shown that the number and distribution of osmiophilic droplets on the epithelial cells are different in different stages. In the initial stage, not many osmiophilic droplets are mainly on ER and the plastid membrane, which does not exist on Golgi bodies and mitochondria. It is implied that osmiophilic droplets are first synthesized on ER. Although the amount of synthesis is not much, it is secreted through plastid membranes. With the development of resin ducts, more and more osmiophilic droplets emerge, which also emerge on plastids, mitochondria and Golgi bodies. After resin ducts get matured, not only the amount of osmiophilic droplets on plastids, mitochondria, ER and Golgi bodies increases, but there are also a lot of osmiophilic droplets in the cytoplasm on both sides of plasmalemma and cell walls. ER in cytoplasm often connects with plastids and plasmalemma. It can be concluded that, with the development of resin ducts, the ability of resin synthesis improve. Plastids are the primary place for synthesis. ER plays an important role of transportation.

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