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芝麻核雄性不育系 ms86-1 小孢子败育过程的超微结构

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摘 要: 运用透射电子显微镜对芝麻核雄性不育系 ms86-1 的可育和不育花药进行了超微结构的比较观察。根据小孢子的细胞学形态特征, 将芝麻花粉发育过程划分为小孢子母细胞形成期、减数分裂期、四分体期、单核小孢子早期、单核小孢子中期、单核小孢子晚期、花粉成熟期 7 个时期。对比观察表明芝麻核雄性不育的败育迹象起始于小孢子母细胞形成期, 并伴随着进一步发育, 败育现象逐渐明显, 小孢子母细胞形成期小孢子母细胞壁形状不规则; 减数分裂期小孢子母细胞壁严重扭曲变形, 质膜外缺少早期外壁成分——原基粒棒; 四分体期胼胝质壁外沉积物异常, 呈绒毛状; 四分体解体后形成畸形小孢子, 孢子外壁不健全, 绒毡层异常肥厚、降解延迟, 释放极少量的畸形乌氏体; 随后小孢子愈发皱缩, 胞质凝集, 内含物减少并逐渐凝聚成一团电子致密物质, 最终走向完全败育。本研究揭示了不育小孢子的败育过程和败育特征, 为深入研究芝麻核雄性不育败育机理奠定了基础。

关键词: 芝麻; 核雄性不育; 小孢子发生; 超微结构; 透射电子显微镜

Ultrastructure in Microspore Abortion of Genic Male Sterile Line in Sesame (*Sesamum indicum* L.)

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Abstract: Sesame (*Sesamum indicum* L.) is an important oil-seed crop with great nutritional value, and the sesame hybrid has remarkable heterosis in many characters, especially in productivity. To investigate the abortion mechanism of genic male sterile (GMS) line in sesame, a comparative study was conducted on the fertile and sterile microsporogenesis of ms86-1 derived from the male sterile line discovered by Osman using transmission electron microscopy (TEM) techniques. According to the morphologic characteristics of the microspores, the developmental process of sesame pollen could be tentatively divided into seven stages, including microsporocyte formation stage, microsporocyte meiosis stage, tetrad stage, early microspore stage, middle microspore stage, late microspore stage, and pollen maturation stage, respectively. The abnormal phenomena observed in the sterile anthers indicated that male sterility might arise in microsporocyte formation stage. With the growth and development of the sterile anthers, the following abnormal features were observed evidently. The cell wall of the sterile microsporocytes was irregular during their formation stage. In the meiosis stage, the cell walls were getting distorted obviously, and the microsporocytes failed to form the early exine component designated as probaculums on the outside of the plasma membrane. Subsequently, abnormal villiform deposits were observed on the outside of the callose wall during the tetrad stage. As soon as the tetrad cells disintegrated, the released sterile microspores represented aberrantly dumbbell-shaped, and their exines were undergrown without any baculum. Accompanying with the delay of the degeneration process, inclusions of the tapetum cells became more abundant and few abnormal ubisch bodies were secreted. Later on, the sterile microspore was gradually crimpled as its cytoplasm agglomerated to an electron dense clot, and ultimately degraded to the complete abortion. In this paper, compared with the fertile pollen development, the abortion process and characteristics of the sterile anthers were disclosed, providing a foundation for the greater insight into the

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abortion mechanism of GMS line in sesame.

Keywords: Sesame (*Sesamum indicum* L.); Genetic male sterility; Microsporogenesis; Ultrastructure; TEM

芝麻(*Sesamum indicum* L., 2*n*=26)属于胡麻科芝麻属, 是世界上重要的油料作物之一。1945 年印度学者 Pal 首次报道了芝麻的杂种优势[1], 随后许多学者研究证实芝麻品种间杂交 F_1 在产量方面杂种优势尤为明显[2], 在品质、抗逆性等方面也具有较强的超标优势[3]。1982 年 Osman 与 Yermanos[4]报道了第一个可利用的芝麻核雄性不育材料, 并认为核雄性不育性状受一对隐性基因控制。1983 年河南省芝麻研究中心将其引入后, 通过回交改良选育出国内外第一个有实用价值的核雄性不育系 ms86-1, 并应用于二系杂交制种[5], 但二系制种须在初花期拔除一半可育株, 存在工作量大、纯度无法保证等问题而难以在生产上大面积应用。因此, 深入研究核雄性不育机理, 改进杂交制种方法, 对芝麻杂种优势利用具有重要意义。高洪善等[6]1992 年对芝麻核不育系小孢子发育过程进行了初步观察, 指出小孢子败育发生在四分体之后的无液泡小孢子期, 绒毡层异常是败育的直接原因, 但文章主要侧重于对四分体以后败育现象的描述。到目前为止, 对芝麻核雄性不育小孢子败育过程尚缺乏全面系统的细胞学认识。本研究以 ms86-1 为材料, 通过透射电子显微镜系统观察可育和不育小孢子发育过程, 以期进一步明确芝麻核不育小孢子的败育过程和超微结构特征, 为芝麻雄性不育机理及应用研究提供依据。

1　材料与方法

芝麻核雄性不育系 ms86-1 由河南省农作物新品种重点实验室提供。2007 年 5 月种于河南农科院试验田, 常规管理。

于盛花期根据花药特征鉴别可育株和不育株, 可育株花药白色、饱满, 开裂时散出大量花粉; 不育株花药扁平、绿色半透明状, 无花粉不开裂。每天早上分别对可育株和不育株进行定株取样观察, 结合常规镜检, 依花序从上到下的顺序, 从每株顶端摘取着生位置相同的花蕾(即按花蕾从小到大发育相差一天的顺序取样), 花蕾长 2 mm 以下为第一组, 2 mm 以上按相隔 1 mm 分组。花蕾离体后立即剥取花药, 并投入预冷的 3% (pH 7.2) 戊二醛抽气固定; 0.1 mol L^{-1} 磷酸缓冲液漂洗 3 次, 固定于 1%锇酸水溶液中; 再用 0.1 mol L^{-1} 磷酸缓冲液漂洗 3 次, 经梯度浓度丙酮脱水, 环氧树脂 Epon 812 浸透、包埋、聚合; Power Tome-XL 型超薄切片机上切成厚度为 70 nm 的切片,醋酸双氧铀和柠檬酸双重染色; 最后于日立 H-7650 透射电子显微镜下观察、摄影并记录。

2　结果与分析

2.1　芝麻花粉发育时期划分

通过大量芝麻花药显微结构观察和分析,并参照拟南芥、水稻等作物花粉发育过程的分期方法[7-9], 以芝麻小孢子细胞的形态结构为依据, 初步将芝麻花粉发育过程分为 7 个时期(表 1)。

表 1　芝麻花粉发育过程分期

Table 1　Pollen developmental stages in *S. indicum* L.

No.	时期 Stage	花蕾长度 Bud length(BL)(mm)
1	小孢子母细胞形成期 Microsporocyte formation stage	BL＜2
2	减数分裂期 Meiosis stage	2≤BL＜3
3	四分体期 Tetrad stage	3≤BL＜4
4	单核小孢子早期 Early microspore stage	4≤BL＜5
5	单核小孢子中期 Middle microspore stage	5≤BL＜6
6	单核小孢子晚期 Late microspore stage	6≤BL＜7
7	花粉成熟期 Pollen maturation stage	BL≥7

2.2　可育与不育花药的对比观察

2.2.1　*小孢子母细胞形成期*　　从横切面看, 可育花药雄蕊原基已分化出 4 层, 从外到内依次是表皮、药室内壁、中层和绒毡层。中层由 3 层细胞组成; 绒毡层细胞呈长方形, 排列整齐, 核大, 核仁染色明显, 有的细胞含有两个或多个核, 细胞器含量少, 具有较大液泡, 与其他壁层细胞的形态相似(图 1-a)。药壁细胞之间、小孢子母细胞之间存在胞间通道(图 1-c 箭头所示)。小孢子母细胞的形态与周围的药壁细胞明显不同, 细胞排列整齐而有序, 细胞壁形状规则, 细胞核大, 核仁染色明显(图 1-b); 细胞质浓厚, 含丰富的线粒体、核糖体、质体、内质网, 没有明显的液泡(图 1-c)。不育花药的药壁细胞形态(图 1-d)及小孢子母细胞中细胞器含量(图 1-f)与可育花药基本相同, 但小孢子母细胞壁形状不规则, 呈弯曲状, 在小孢子母细胞和绒毡层细胞之间常见一些异常的胞状物质(图 1-e 箭头所示)。

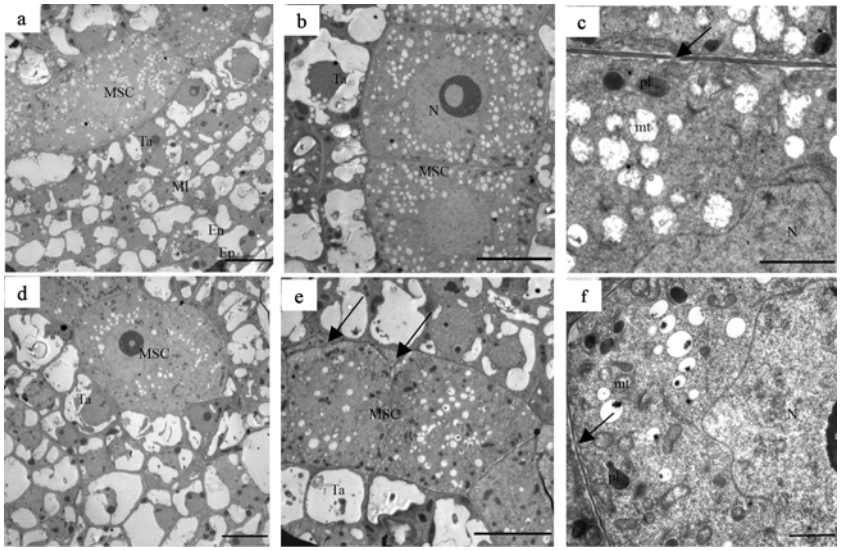

图 1 小孢子母细胞形成期

Fig. 1 Microsporocyte formation stage

MSC：小孢子母细胞; Ta：绒毡层; Ml：中层; En：药室内壁; Ep：表皮; N：细胞核; td：四分体; mt：线粒体; pl：质体; C：胼胝质; Ms：小孢子; V：液泡; ER：内质网; Ub：乌氏体; L：脂质小球。图片均为花药横切面。a：可育小孢子母细胞及四层花药壁细胞; b：可育小孢子母细胞壁形状规则; c：可育胞质内含物和胞间通道(箭头所示); d：不育小孢子母细胞及花药壁细胞; e：不育小孢子母细胞壁形状异常(箭头所示); f：不育胞质内含物和胞间通道(箭头所示)。图中的标尺长度为 100 μm (a, b, d, e), 20 μm (c, f)。

MSC: microsporocyte; Ta: tapetum; Ml: middle layer; En: endothecium; Ep: epidermis; N: nucleus; Td: tetrad; mt: mitochondria; pl: plastid; C: callose; Ms: microspore; V: vacuole; ER: endoplasmic reticulum; Ub: ubisch bodies; L: lipid globule. All photographs are cross-section of anthers.

a: fertile microsporocytes and four layer cells of anther wall; b: regular cell wall between the fertile microsporocytes; c: cytoplasmic inclusions in the fertile microsporocyte and the intracellular channel (shown by arrow); d: sterile microsporocytes and anther wall cells; e: irregular cell wall between the sterile microsporocytes (shown by arrows); f: cytoplasmic inclusions of the sterile microsporocyte and the intracellular channel (shown by arrow). Bars= 100 μm (a, b, d, e), 20 μm (c, f).

2.2.2 *减数分裂期* 可育小孢子母细胞壁外侧逐渐积累薄厚不一的胼胝质(图 2-a), 并在胼胝质和质膜之间出现一圈不连续的黑色鼓槌状物质(图 2-b 箭头所示), 这是小孢子外壁的最早沉淀物——原基粒棒。此时小孢子母细胞中开始出现脂质小球, 质体减少(图 2-c)。绒毡层细胞径向伸长, 内切向壁及径向壁开始弯曲并溶解成不连续状, 原生质体开始浓缩, 周边出现“空腔”(图 2-a), 浓缩的细胞质内含有脂质小球及丰富的线粒体、内质网、核糖体。不育小孢子母细胞之间也开始积累薄厚不一的胼胝质, 细胞壁扭曲变形加剧(图 2-e), 在壁弯曲处, 常见质壁分离形成的空腔(图 2-e 箭头所示), 细胞质中液泡显著增多(图2-f)。绒毡层也出现异常迹象, 许多绒毡层细胞中的小液泡合并成大液泡, 并且将核挤至远离小孢子母细胞的一侧(图 2-d)。

2.2.3 *四分体期* 可育四分孢子被共同的胼胝质包围(图 3-a), 壁外侧出现一层有缺口的电子致密带, 其上沉积了大量的黑色箭状物质(图 3-b)。四分孢子中细胞器含量丰富, 质体高度发育, 质体内部明显可见一些电子密度较高的物质(图 3-c)。绒毡层胞质进一步浓缩成一团, 着色很深, “空腔”增大(图 3-a)。不育四分孢子形成后也被共同的胼胝质包围, 壁外侧也见有一层带缺口的电子致密带, 但其上沉积了大量茸毛状物质(图 3-e)。与可育四分孢子比其细胞器较少, 液泡明显多, 可见液泡吞噬现象(图 3-f)。绒毡层细胞径向伸长, 胞质浓缩, 但大部分浓缩于远离四分体的一侧(图 3-d)。

2.2.4 *单核小孢子早期* 可育小孢子解离后, 呈近球形, 核位于细胞中央(图 4-a)。小孢子外壁物质迅速沉积, 基粒棒发育成熟, 呈短粗的鼓槌状(图 4-b 箭), 外壁外侧开始覆盖孢粉素物质, 萌发孔雏形可见, 至此外壁基本形成; 细胞质内含有丰富的线粒体及发达的质体, 并形成了个别小液泡(图 4-b)。绒毡层细胞径向收缩, 细胞壁完全溶解, 胞质内含物开始降解, 褶皱的绒毡层膜出现, 在膜凹陷处出现乌氏体(图 4-c); 内质网高度发达, 两片层之间的槽库膨大, 内部充满基质(图 4-d); 孢粉素物质形成并分泌, 排放到药室后, 沉积在乌氏体上或直接沉积到小孢子外壁上, 参与外壁的构成。不育小孢子解离后呈“哑铃”状畸形, 核位于细胞中央(图

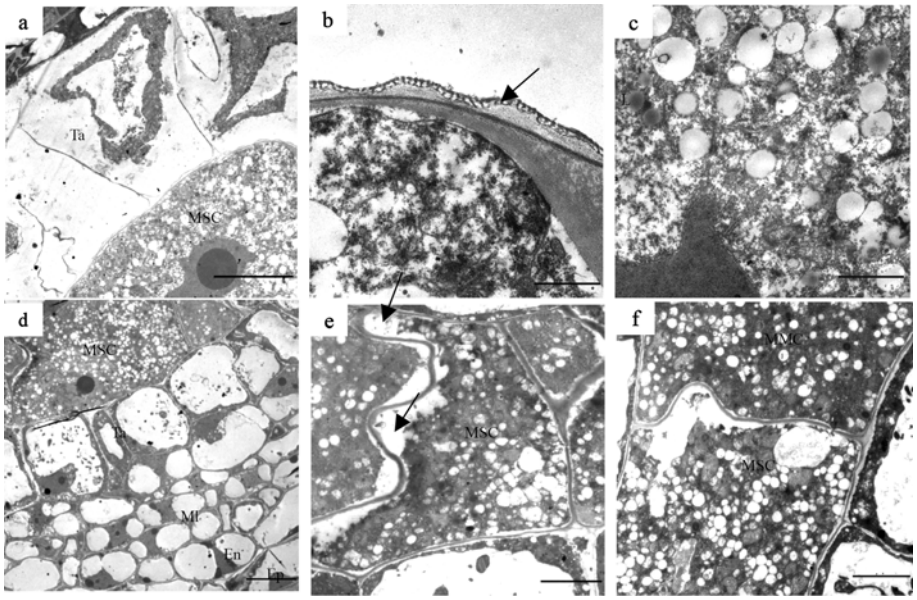

图 2　减数分裂期

Fig. 2　Meiosis stage

a：可育小孢子母细胞及胞质凝集的绒毡层细胞; b：在可育小孢子质膜外形成花粉外壁的原基粒棒结构(箭所示); c：可育小孢子母细胞中质体减少，出现脂质小球; d :不育小孢子母细胞及具中央大液泡的绒毡层细胞; e :不育小孢子母细胞壁扭曲严重，在壁弯曲处，质壁分离出现空腔(箭头所示); f：不育小孢子母细胞中液泡增多。图中的标尺长度为 100 μm (a, d), 10 μm (b), 20 μm (c), 50 μm (e, f)。

a: fertile microsporocyte and tapetal cells with agglomerate cytoplasmic inclusions; b: probacula forming on the outside of the fertile microsporocyte's plasma membrane (shown by arrow); c: fertile microsporocyte with lipid globules and less plastids; d: sterile microsporocyte and tapetal cells with large central vacuoles; e: distorted cell walls of sterile microsporocytes and the lacuna between cell wall and plasma membrane at the crooked location (shown by arrows); f: more vacuoles in the sterile microsporocyte. Bars=100 μm (a, d), 10 μm (b), 20 μm (c), 50 μm (e, f).

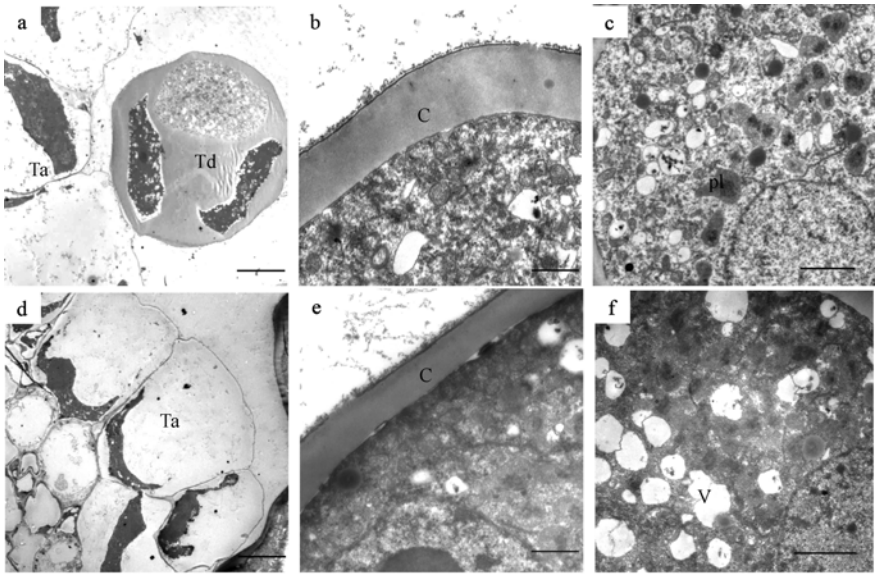

图 3　四分体期

Fig. 3　Tetrad stage

a：可育四分体细胞被厚厚的胼胝质包裹，绒毡层细胞质凝聚在细胞中央; b：可育胼胝质壁外侧出现一层有缺口的电子致密带，其上沉积了大量的黑色箭状物质; c：可育四分孢子中富含发达的质体; d：不育四分体时期绒毡层细胞质凝聚在远离四分体的一侧; e：不育胼胝质壁外侧出现一层有缺口的电子致密带，其上沉积了大量的黑色绒毛状物质; f：不育四分孢子中液泡丰富。图中的标尺长度为 100 μm (a, d), 10 μm (b, e), 20 μm (c, f)。

a: fertile tetrad cells surrounded by thick callose wall and tapetal cytoplasm concentrated in the cell centre; b: a electron dense line with several gaps outside the fertile callose wall and lots of arrow-like objects on its surface; c: fertile tetrad cytoplasm with abundant developed plastids; d: sterile tapetal cytoplasm concentrated at the side far from the tetrad cells; e: a electron dense line with several gaps outside the sterile callose wall and lots of abnormal villiform objects on its surface; f: sterile tetrad cytoplasm with numerous vacuoles. Bars=100 μm (a, d), 10 μm (b, e), 20 μm (c, f).

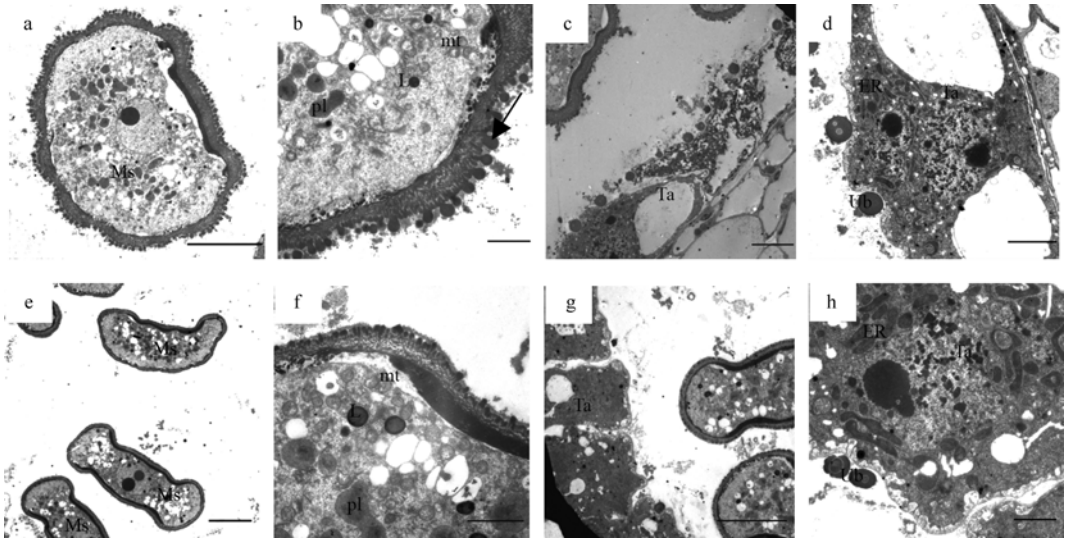

图 4 单核小孢子早期

Fig. 4 Early microspore stage

a：可育小孢子呈近球形，细胞核位于中央，细胞质中含有丰富的线粒体和发达的质体；b：可育小孢子外壁基本形成，基粒棒发育(箭头所示)；c：可育花药绒毡层细胞开始降解，乌氏体开始分泌；d：可育绒毡层细胞中含有发达的内质网；e：不育小孢子呈哑铃状畸形，细胞核位于中央，细胞质中含有丰富的线粒体和发达的质体；f：不育小孢子外壁发育不健全，缺少基粒棒；g：不育绒毡层细胞肥厚、不降解，分泌极少量的畸形乌氏体；h：不育绒毡层细胞中含有发达的内质网。图中的标尺长度为 100 μm (a, c, e, g), 20 μm (b, f, h), 50 μm (d)。

a: near-spherical fertile microspore, nuclear located in the center and cytoplasm possessed abundant mitochondria and developed plastids; b: fertile microspore exine outline established with many bacula (shown by arrow); c: fertile tapetal cells disintegrated and many ubisch bodies secreted; d: fertile tapetal cells with well-developed endoplasmic reticulum; e: abnormally dumbbell-shaped sterile microspores, nucleus located in the center and microspore cytoplasm possessed abundant mitochondria and developed plastids; f: sterile exine without baculum; g: sterile tapetal cells contained abundant inclusions and few abnormal ubisch bodies secreted; h: sterile tapetal cells with well-developed endoplasmic reticulum. Bars= 100 μm (a, c, e, g), 20 μm (b, f, h), 50 μm (d).

4-e)。小孢子外壁物质也迅速沉积，但与可育小孢子外壁存在明显差异，尤其是缺少基粒棒；细胞质内含物与可育者相似，含有丰富的线粒体和发达的质体(图 4-f)。此时绒毡层壁也完全溶解，出现绒毡层膜，但绒毡层细胞变得肥厚，内含物丰富，不发生收缩和降解现象，仅分泌极少量的畸形乌氏体(图 4-g)，细胞质中内质网高度发达、槽库膨大，也观察到孢粉素合成分泌现象(图 4-h)。

2.2.5 *单核小孢子中期* 可育小孢子中液泡增多，并逐渐合并成较大的液泡，但尚未形成中央大液泡，细胞核被挤到边侧，细胞质中细胞器很少，并贴向细胞的周边，主要含有线粒体；小孢子外壁没有明显变化，仅是外壁物质沉积更加致密(图 5-a)。绒毡层细胞降解为山丘状，细胞核的核膜、核仁消失，分泌大量乌氏体，绒毡层膜变化不大(图 5-b)。不育小孢子中内含物显著减少并开始凝集(图 5-f)。绒毡层内含物丰富、不降解，仅发生一些径向收缩，分泌极少量畸形乌氏体(图 5-g)。

2.2.6 *单核小孢子晚期* 可育小孢子中的液泡合并成中央大液泡，细胞核仍位于细胞边侧，细胞质中细胞器增多，出现了大量核糖体(图 5-c)；在花粉外壁内侧和质膜之间逐渐积累内壁物质(图 5-c 箭头所示)。绒毡层细胞进一步降解，内含物显著减少，乌氏体分泌量也开始减少，绒毡层膜仍然可见(图 5-d)。不育畸形小孢子的细胞质凝聚成一团电子致密物质。绒毡层细胞出现降解迹象，如径向收缩明显，内含物开始凝集(图 5-h)。

2.2.7 *花粉成熟期* 可育小孢子中的中央大液泡逐渐变小至消失，细胞内含物逐渐增多至布满整个细胞，小孢子经过不对称有丝分裂形成成熟花粉粒；花粉粒的内壁物质在局部向内侧扩展并显著增厚，萌发孔形成，芝麻花粉粒通常含有多个萌发孔(图 5-e 箭头所示)。绒毡层细胞降解至基本消失(图 5-e)。不育小孢子细胞进一步皱缩，内含物仍凝聚成一团电子致密物质。绒毡层细胞中出现大液泡，细胞质内含物开始减少(图 5-i)。

3 讨论

3.1 小孢子母细胞壁形状不规则与雄性不育的关系

植物雄性配子体的发生起始于花药原基的分化发育，这一过程涉及多次细胞分裂，受到一系列基

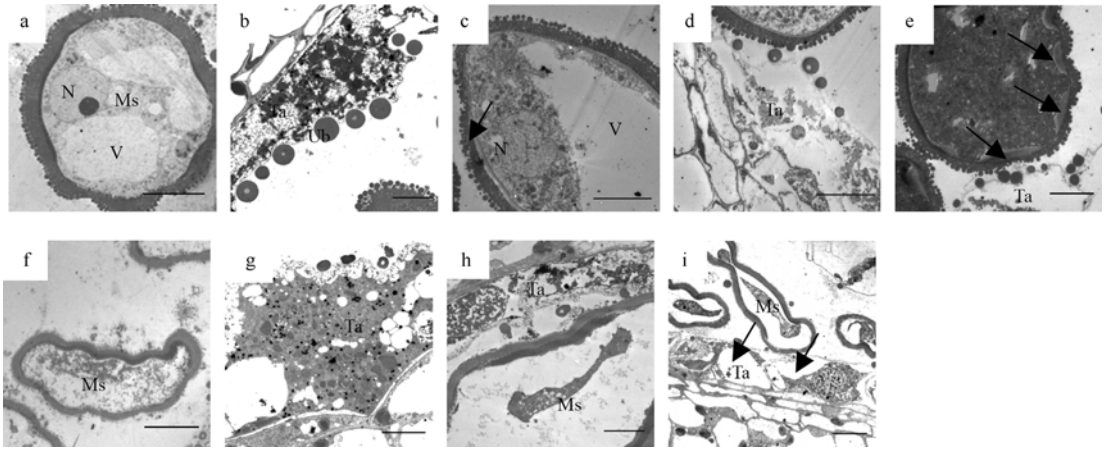

图 5　单核小孢子中期—花粉成熟期

Fig. 5　Middle microspore stage–pollen maturation stage

a：可育单核中期球形小孢子，细胞内形成较大液泡，细胞核位于边侧，细胞器减少; b：可育单核中期绒毡层细胞降解成山丘状，分泌大量乌氏体; c：可育单核晚期小孢子，中央大液泡形成，积累内壁物质(箭头所示); d：可育单核晚期绒毡层细胞内含物稀少; e：可育成熟花粉粒，多个萌发孔形成(箭所示); f：不育小孢子内含物稀少并开始凝集; g：不育小孢子绒毡层细胞仅发生一些径向收缩，内含物丰富、不降解; h：不育小孢子内含物凝聚成一团，绒毡层细胞质凝集; i：不育小孢子愈发皱缩，绒毡层细胞中出现“空腔”、胞质内含物减少(箭头所示)。图中标尺长度为 100 μm (a, c, d, e, f, i), 50 μm (b, g, h)。

a: fertile middle microspore stage, spherical microspore with several large vacuoles, nuclear and less organelles locating at the edge of the cell; b: fertile middle microspore stage, further disintegrated tapetal cells being concave or wavy with abundant ubisch bodies secreted; c: fertile late microspore stage, microspore with a large central vacuole and some intine substance(shown by arrow); d: fertile late microspore stage, tapetal cells with sparse cytoplasm; e: fertile mature pollen with several apertures (shown by arrows); f: sterile middle stage microspore with sparse and agglomerate cytoplasm; g: narrower sterile tapetal cells with abundant cytoplasm; h: sterile microspore cytoplasm inclusions agglomerated to a clot and the tapetal cytoplasm initiated agglomerate; i: crimpled sterile microspores and the tapetal cells with less cytoplasm inclusions and large blank regions (shown by arrows). Bars= 100 μm (a, c, d, e, f, i), 50 μm (b, g, h).

因的精确调控，分化过程的异常可能注定小孢子败育的命运。近几年已经克隆出一些控制孢原细胞分化的基因，如拟南芥中的 *EXS/EMS1* [10-11]、水稻中 *MSP1* [12]、玉米中 *MAC1*[13]，这些基因主要控制雄蕊发育中造孢细胞的数量，这些基因的突变将产生过多的小孢子母细胞、花药壁细胞混乱或缺失，导致雄性不育。本研究发现，不育花药中最早显示出的异常现象是大量小孢子母细胞壁形状不规则，这可能是特定基因调控初生造孢细胞异常分裂或异常排列所致。伴随进一步发育，减数分裂期小孢子母细胞壁扭曲变形严重，在壁弯曲处质壁分离出现空腔，这种空腔是否会造成细胞内外的物质信息交换受阻，即造成小孢子母细胞营养吸收受阻或早期孢壁成分运输受阻而最终导致败育尚需生理学、遗传学的证据。

3.2　小孢子外壁发育异常及绒毡层延迟降解与雄性不育的关系

高洪善等[6]基于四分体后的败育现象指出，芝麻花药绒毡层发育异常如不分泌乌氏体会导致小孢子外壁形成受阻，进而导致小孢子皱缩退化。但本研究观察到，早在减数分裂期不育小孢子母细胞的外壁发育就显现出异常，即缺少原基粒棒，由于此时绒毡层还未降解，早期外壁成分缺失应与小孢子母细胞发育异常密切相关。许多有关花粉外壁发育的研究表明早期花粉外壁物质只由小孢子母细胞提供，当小孢子各个分离以后，壁物质除来源于小孢子本身外，还由绒毡层细胞提供[14]。Chapman[15]认为由小孢子本身产生的早期初生外壁提供了外壁发育的模式，指导着孢粉素物质的沉积。卢永根等[16]指出即使绒毡层发育正常，适时地分泌孢粉素物质，但如果小孢子本身异常，无法提供外壁发育的模式，致使孢粉素异常沉积，同样会导致花粉败育。

绒毡层作为药壁的最内层，对花粉发育的整个过程有着重要作用，绒毡层细胞的异常必然会影响小孢子的正常发育。在花粉正常发育中，绒毡层细胞的适时解体是一种细胞程序化凋亡的过程，这种凋亡程序受严格的遗传信息调控[17-18]。谢潮添等[19]通过对白菜雄性不育的超微结构研究指出绒毡层的降解受来自生殖细胞的信号调控，败育的小孢子可能因为营养需求大大减少而导致绒毡层细胞不降解或延迟降解。本研究观察到小孢子母细胞形成期绒毡层正常、单核期延迟降解，而小孢子母细胞壁不

规则、花粉外壁起始发育受阻等异常现象先于绒毡层异常发生，我们推测小孢子母细胞早期的异常可能释放某种信号导致绒毡层细胞的程序化降解过程推迟、不能正常分泌乌氏体，而绒毡层的异常进一步促进了小孢子的败育。

4 结论

芝麻核雄性不育材料 ms86-1 的败育迹象起始于花粉母细胞形成期，伴随小孢子进一步发育，败育现象越来越明显。其显著特征是，早期小孢子母细胞壁形状异常，并逐渐加剧扭曲变形，出现质壁分离现象；小孢子外壁发育不健全，缺少基粒棒；四分体解体后形成畸形小孢子，绒毡层延迟降解；畸形小孢子经过胞质浓缩而彻底败育。

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