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温室栽培黄金梨种子败育初探

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摘 要:【目的】通过比较温室栽培和露地栽培黄金梨从萌芽期至开花期的胚珠、胚囊发育情况,初步探讨温室栽培黄金梨种子败育的原因。**【方法】**调查记录了温室、露地栽培黄金梨萌芽期至开花期的气温变化规律,并以2种栽培条件下的黄金梨为试材,对该时期的花芽进行采样,利用石蜡切片法对比观察黄金梨的胚珠、胚囊发育过程及其形态特点,并用测微尺测量了开花期胚珠、胚囊的大小;于花后20 d统计坐果率,并对成熟期的果实进行种子败育情况调查。**【结果】**露地栽培黄金梨种子败育率低,坐果率高,温室黄金梨种子败育率高,坐果率低。温室栽培条件下,不适宜的高温处理缩短了黄金梨从现蕾到开花所需时间;同时造成开花期胚囊发育滞后,胚囊发育不完全(未成熟),50%的胚囊仍处于单核、二核阶段,11.1%的胚囊处于四核阶段,且胚囊的长度和宽度均小于露地黄金梨。**【结论】**温室黄金梨种子败育率高、坐果率低的重要原因是开花前的高温处理导致胚囊发育滞后、发育不完全。

关键词:黄金梨;温室;种子败育;胚囊;显微观察

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Preliminary study on seed abortion of Whangkeumbae pear cultivated in the greenhouse

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Abstract:【Objective】The Whangkeumbae pear had high early yield and good quality, and when cultivated in the greenhouse, it could prolong the fruit supply period and increase the economic benefits to fruit growers. However, in the production, it was found that the fruit setting rate of Whangkeumbae pear cultivated in the greenhouse was low, the incidence of malformed fruit was high, and most of the dropped and malformed fruits were seedless. Previous studies found that although Whangkeumbae pear had little or no pollen, the pistil could develop normally, and the fruit setting rate could be improved by artificial pollination. However, under the greenhouse cultivation conditions, abnormal temperature regulation was easy to cause abnormal development of ovules and embryo sacs, which caused seed abortion. So, by comparing the development of ovule and embryo sac in the same phenological period of Whangkeumbae pear cultivated in the greenhouse and open field, and combing with the pattern of temperature change, this paper preliminarily discussed the cause of seed abortion of Whangkeumbae pear cultivated in the greenhouse.【Methods】This paper investigated and recorded the pattern of temperature change from bud break to flowering of Whangkeumbae pear cultivated in the greenhouse and open field, and took Whangkeumbae pear under two cultivation conditions as test materials. The flower buds from germination stage to anthesis stage were sampled, and the development process and morphological characteristics of ovules and embryo sacs of Whangkeumbae pear during this period were compared and observed by paraffin sectioning. The ovule and embryo sac size of Whangkeumbae pear at flowering stage

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were measured with a micrometer. The fruit setting rate was calculated 20 days after anthesis stage, and the seed abortion of fruits during maturation period was investigated.【Results】The seed abortion rate of Whangkeumbae pear cultivated in the greenhouse was 62.0%, which was significantly higher than that cultivated in the open field (7.0%). And its fruit setting rate was 21.5%, which was significantly lower than that cultivated in the open field (51.5%). Under the condition of open cultivation, the abortion rate of Whangkeumbae pear seeds was only 7%, with an average of 9.3 normal seeds in each fruit, and seeds were found in five ventricles. Under greenhouse cultivation, the abortion rate of Whangkeumbae pear seeds was as high as 62%, and each fruit had only 3.8 seeds on average, and only 2.7 ventricles had seeds. Comparing the temperature under two cultivation conditions, it was found that the maximum temperature in the greenhouse during the day was generally higher than that in the open field. The average maximum temperature in the greenhouse from bud break to flowering was from 19.6 ℃ to 22.9 ℃, while the open ground was from 14.3 ℃ to 18.6 ℃. Especially 7 days before flowering, the average maximum temperature in the greenhouse during the day was as high as 26.0 ℃, but the open ground was only 19.9 ℃. The unsuitable high temperature treated at the condition of greenhouse cultivation accelerated the flowering speed of Whangkeumbae pear. As a result, the time from bud break to flowering of Whangkeumbae pear cultivated in the greenhouse was 3 days shorter than that cultivated in the open field. At the same time, the embryo sac could not mature at anthesis stage, 50% of the embryo sac was still at single nucleus embryo sac and bi-nucleate embryo sac stage, and 11.1% of the embryo sac was at tetra-nuclear embryo sac stage. When Whangkeumbae pear cultivated in the open field entered the flowering stage, 73.3% of the embryo sacs completed differentiation, but the rest were in different multi-nucleated embryo sac stage, and single nucleus, bi-nucleate and tetra-nuclear embryo sac stages were not detected. In the comparative observation on ovule and embryo sac sections of Whangkeumbae pear, it was also found that the length and width of embryo sac of Whangkeumbae pear under greenhouse cultivation (42.9 μm, 21.8 μm) were less than those under open ground cultivation (78.4 μm, 32.9 μm), and the coefficient of variation was large.【Conclusion】The high temperature treatment before flowering accelerated the flowering speed of Whangkeumbae pear, which resulted in delayed embryo sac development, and the degree of embryo sac development was not synchronized with the flowering period. The retardation of Whangkeumbae pear embryo sac development at anthesis stage was the important reason for high seed abortion and low fruit setting rates in the greenhouse.

Key words: Whangkeumbae pear; Greenhouse; Seed abortion; Embryo sac; Microscopic observation

黄金梨早期丰产性强，品质优良，但耐贮藏性较差，冷藏条件下，一般只能贮藏3~4个月[1]。温室栽培技术可充分发挥该品种的两大优势，延长果实供应期，增加果农的经济效益。但在生产中发现，温室栽培条件下黄金梨坐果率低，畸形果发生率高，在对温室落果、畸形果进行剖切过程中发现，多数果核内无种子。种子发育的任一方面，如胚珠、胚囊、花粉、授粉受精、胚、胚乳等发育过程受阻都可能引起种子败育[2]。而种子的前身是胚珠，胚珠是胚囊的携带者，胚珠发育过程中如出现形态结构异常、大孢子母细胞发育不完全或退化，都易导致植物雌性器官育性降低或不育[3]。边卫东等[4]曾对黄金梨的胚珠及花粉发育过程进行了切片观察，研究发现黄金梨从萌芽到花蕾期（开花前 14 d），胚珠原基已分化出珠被和珠心，小孢子母细胞减数分裂后形成的四分体出现率达73.0%，并有早期花粉粒出现（27%）；到开花前 7 d，大孢子母细胞形成，胚珠分化完全，但早期花粉粒液泡化；到开花期胚囊形成，花药空囊。可见，黄金梨虽然无花粉或花粉极少，但雌蕊能正常发育，在栽培生产中如合理配置授粉树，则能有效解决花粉败育问题，提高坐果率。在授粉试验中发现八月酥、绿宝石、早酥梨均可作为黄金梨的授粉品种[5-6]。

此外，结合观察黄金梨[4]和甜樱桃[7-8]的胚珠及花粉发育过程发现，二者的胚珠、胚囊发育过程类

似，其胚珠原基均在开花前14 d分化出珠心与珠被，且在开花期胚囊已经形成。同时，在观察甜樱桃的胚珠与温度变化相关性的过程中发现，甜樱桃胚囊的发育是在较低温度下完成，胚囊形成期平均最高温度为20.6 ℃，最低温度为7.9 ℃。在温室促成栽培条件下，温度的调控占主导地位，温度调控失常容易造成胚珠、胚囊发育异常，引起种子败育。为此，笔者从温室栽培黄金梨胚珠发育与温度变化的关系入手，对比调查了露地、温室栽培条件下气温变化规律、黄金梨的坐果率、种子败育率，以及同一物候期黄金梨的胚珠、胚囊发育过程，以求探明温室黄金梨种子败育率高、坐果率低的原因及其解决方法。

1　材料和方法

1.1　材料

试材取自河北科技师范学院园艺实验站日光温室梨及露地梨新品种栽培区。日光温室跨度7.0 m，脊高3.45 m，长62 m，温室内主栽品种为黄金梨，树龄为8年生，授粉品种有八月酥、绿宝石、早酥梨、黄冠，授粉树比例为30%。2020年1月1日温室升温，开花期为2月5—12日，6月下旬—7月上旬果实成熟。露地梨栽培区，黄金梨树龄均为8年生，开花期为4月15—22日，9月上旬果实成熟。

1.2　方法

1.2.1　温度观察　在露地栽培区，距地面1.5 m高处随机安装3个百叶箱，在温室栽培区的东、中、西部分别安装1个百叶箱，箱内均放置ZDR-20田间数据自动记录仪，每15 min自动采集1次温度数据，记录萌芽期至开花期的温度。

1.2.2　黄金梨坐果率及种子败育率调查　在温室、露地黄金梨萌芽期，分别挂牌选定50个短果枝，记录每个短果枝上的花朵数，在开花期统一进行人工授粉，并于花后20 d调查每个短果枝上坐果数。7月下旬温室黄金梨成熟后随机抽取50个果实与露地果实同期观察。横切果实，调查果实中种子败育情况。

1.2.3　黄金梨胚珠、胚囊解剖观察方法　分别于温室、露地黄金梨萌芽期开始采样，直至开花期，每次随机选取20个顶花芽。温室黄金梨采样日期：1月14日、1月21日、1月28日、2月8日，露地黄金梨采样日期：3月23日、3月30日、4月6日、4月20日。将花芽取下后在室内剥去鳞片，用FAA固定液固定，乙醇系列脱水，做成石蜡切片，番红、固绿对染，制成永久切片，在Olympus DP70显微镜下观察胚珠、胚囊的发育情况及形态特征，并用测微尺测量开花期温室及露地黄金梨的胚珠、胚囊大小。

2　结果与分析

2.1　温室、露地气温比较

如图1所示，温室夜间平均最低温度能保持在6.0 ℃，露地平均最低温度为7.7 ℃。从萌芽期至开花期温室白天平均最高温度为21.2 ℃，露地为16.8 ℃。萌芽期、现蕾期温室白天各阶段平均最高温度为19.6 ℃、22.9 ℃，露地为14.3 ℃、18.6 ℃，尤其是在开花前7 d，温室内白天平均最高温度高达26.0 ℃，露地仅为19.9 ℃。可见，温室白天最高气温普遍高于露地，且在大孢子母细胞形成后（即开花

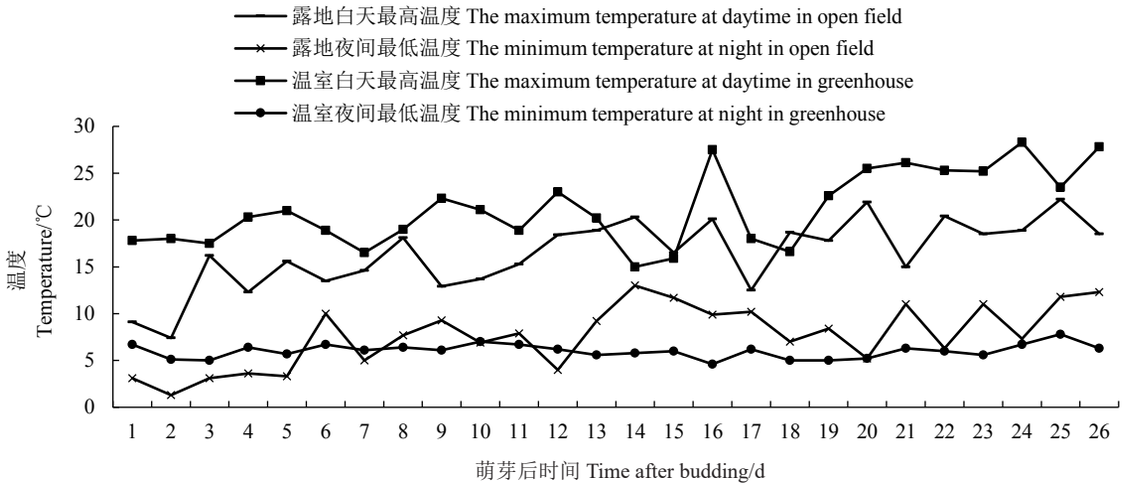


图1　温室、露地温度变化规律

Fig. 1　The changes of temperature in greenhouse and open field

前7 d)平均白天最高气温超过了25 ℃。

2.2 温室、露地黄金梨种子发育及坐果情况

梨属仁果类,正常情况下每个果实有5个心室,每个心室中有2个胚珠,可形成10粒种子。由表1、图2可知,在露地栽培条件下,黄金梨种子败育率仅有7%,每个果实中平均有9.3粒发育正常的种子且5个心室中均有正常种子;温室栽培条件下黄金梨种子败育率高达62%,每个果实平均仅有3.8粒发育正常的种子,5个心室平均仅有2.7个心室中有正常的种子,其中以3个心室和2个心室有正常种子的果实比例最高,分别为32%、30%。温室栽培的黄金梨不仅种子败育率极显著高于露地栽培的黄金梨,而且其坐果率极显著地低于露地栽培的黄金梨。

表1 温室、露地黄金梨果实中种子分布及坐果率

Table 1 The seed distribution and fruit setting rate of Whangkeumbae pear in greenhouse and open field

调查项目 Investigate items	温室 Greenhouse	露地 Open field
每个果实平均有种子的心室数 The average number of locules with seed per fruit	2.7	5.0
每个果实平均种子数 The average number of seeds per fruit	3.8	9.3
5个心室均有种子果实百分率 The percentage of all locules with seed/%	14.0	100.0
4个心室有种子果实百分率 The percentage of four locules with seed/%	6.0	0.0
3个心室有种子果实百分率 The percentage of three locules with seed/%	32.0	0.0
2个心室有种子果实百分率 The percentage of two locules with seed/%	30.0	0.0
1个心室有种子果实百分率 The percentage of one locules with seed/%	18.0	0.0
种子败育率 The seed sterility rate/%	62.0 A	7.0 B
花朵坐果率 The fruit setting rate of flowers/%	21.5 A	51.5 B

注:不同大写字母表示在 $p<0.01$ 差异极显著。

Note: Different capital letters indicate extremely significant difference at $p<0.01$.

图2 露地、温室栽培黄金梨种子败育情况

Fig. 2 The seed sterility of Whangkeumbae pear in greenhouse and open field

2.3 温室、露地黄金梨胚珠发育过程及形态观察

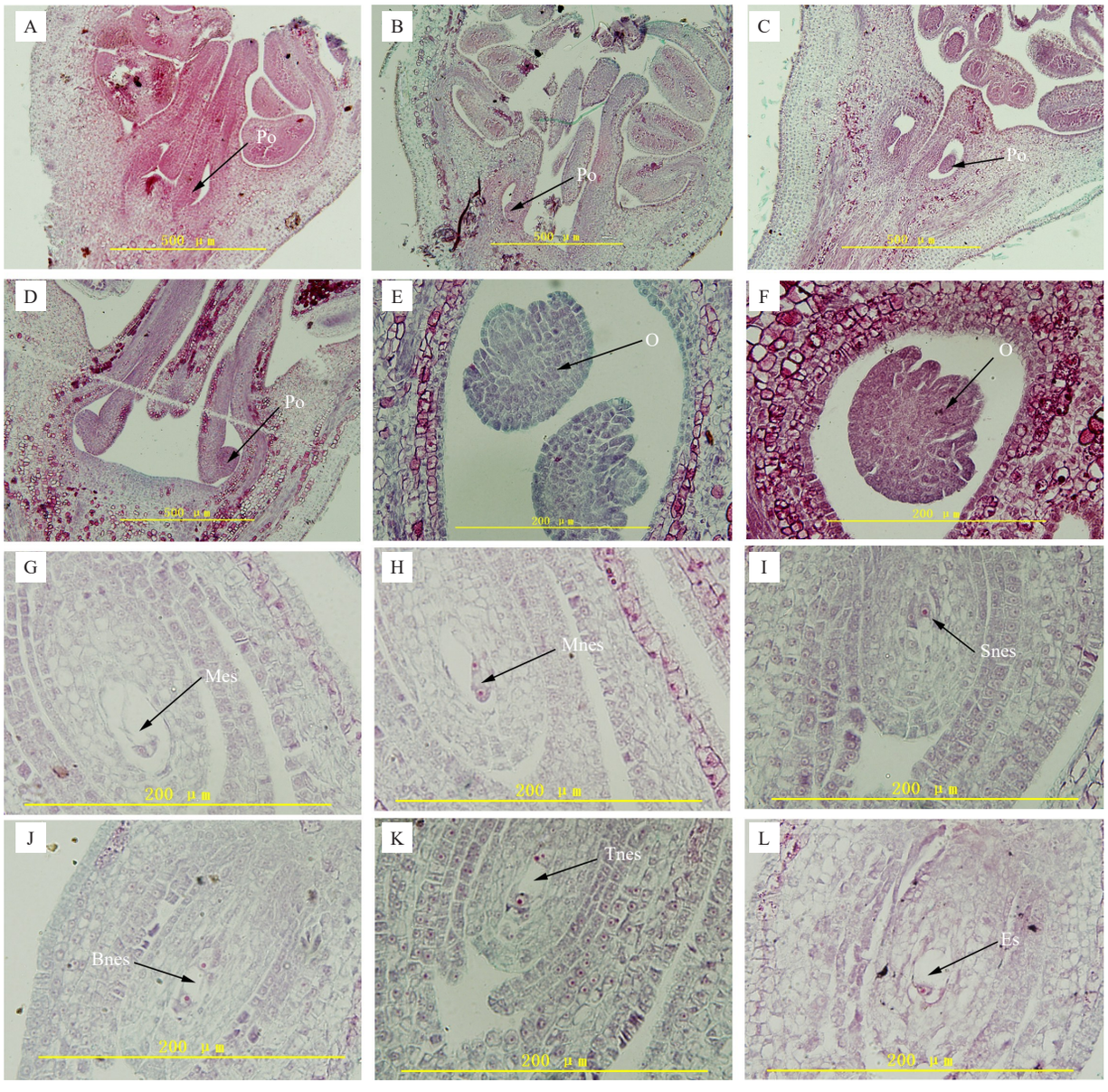
由表2可知,露地栽培条件下,黄金梨从萌芽到开花需要经历28 d;由于栽培黄金梨的温室白天温

表2 温室、露地黄金梨胚珠发育进程

Table 2 The developmental process of ovule of Whangkeumbae pear in greenhouse and open field

温室 Greenhouse			露地 Open field		
萌芽后时间 Time after budding/d	胚珠发育进程 Developmental process of ovule	花芽外部形态 External behavior of flower bud	萌芽后时间 Time after budding/d	胚珠发育进程 Developmental process of ovule	花芽外部形态 External behavior of flower bud
0	胚珠原基出现期 Primordium of ovule appear	花芽鳞松动,芽尖稍开裂(萌芽期) Scales of flower bud loosed, tip of flower bud open edlightly (budding period)	0	胚珠原基出现期 Primordium of ovule appear	花芽鳞松动,芽尖稍开裂(萌芽期) Scales of flower bud loosed, tip of flower bud opened lightly (budding period)
7	胚珠原基 Primordium of ovule	花芽鳞片错开,鳞片间露白,鳞片变浅褐色 Scale of flower bud dehisced and turned light brown, the area between scales appeared white	7	胚珠原基 Primordium of ovule	花芽鳞片错开,鳞片间露白,鳞片变浅褐色 Scale of flower bud dehisced and turned light brown, the area between scales appeared white
14	胚珠分化出珠被与珠心 Integument and nucellus differentiated from ovule	芽鳞开裂鳞片间露白,花蕾露小尖(现蕾期) Scales open, the area between scales appeared white, petal present pinna (the period of flower appeared)	14	胚珠分化出珠被与珠心 Integument and nucellus differentiated from ovule	芽鳞开裂鳞片间露白,花蕾露小尖(现蕾期) Scales open, the area between scales appeared white, petal present pinna (the period of flower appeared)
25	不同核型的胚囊 Embryo sac with vary type of nucleus	开花期 Anthesis	28	成熟胚囊或多核胚囊 Mature embryo sac or more nucleus embryo sac	开花期 Anthesis

度高，高温加快了温室黄金梨的开花速度，使得从现蕾到开花所需时间比露地缩短了3 d。无论是露地还是温室栽培的黄金梨，胚珠原基于萌芽期出现（图3-A~B），到现蕾期（萌芽后14 d），胚珠均已分化出珠被与珠心（图3-E~F）。到开花期，露地栽培黄金梨73.3%的胚囊完成分化（图3-G），其余处于不同的



A. 露地梨萌芽期胚珠原基；B. 温室梨萌芽期胚珠原基；C. 露地梨萌芽后7 d胚珠原基；D. 温室梨萌芽后7 d胚珠原基；E. 露地梨萌芽后14 d胚珠；F. 温室梨萌芽后14 d胚珠；G. 露地梨开花期成熟胚囊；H. 露地梨开花期多核胚囊；I. 温室梨开花期单核胚囊；J. 温室梨开花期二核胚囊；K. 温室梨开花期四核胚囊；L. 温室梨开花期胚囊。Po. 胚珠原基；O. 胚珠；Mes. 成熟胚囊；Mnes. 多核胚囊；Snes. 单核胚囊；Bnes. 二核胚囊；Tnes. 四核胚囊；Es. 胚囊。

A. Primordium of ovule of the pear before budding in open field; B. Primordium of ovule in budding period of the pear in greenhouse; C. Primordium of ovule of the pear 7 days after budding in open field; D. Primordium of ovule of the pear 7 days after budding in greenhouse; E. Ovule of the pear 14 days after budding in open field; F. Ovule of the pear 14 days after budding in greenhouse; G. Mature embryo sac of the pear in anthesis in open field; H. Multi-nucleate embryo sac of the pear in anthesis in open field; I. Single nucleus embryo sac of the pear in anthesis in greenhouse; J. Bi-nucleate embryo sac of the pear in anthesis in greenhouse; K. Tetra-nuclear embryo sac of the pear in anthesis in greenhouse; L. Embryo sac in anthesis of the pear in greenhouse. Po. Primordium of ovule; O. Ovule; Mes. Mature embryo sac; Mnes. Multi-nucleate embryo sac; Snes. Single nucleus embryo sac; Bnes. Bi-nucleate embryo sac; Tnes. Tetra-nuclear embryo sac; Es. Embryo sac.

图3　温室、露地黄金梨胚珠、胚囊萌芽期至开花期解剖观察

Fig. 3　Observation on ovule and embryo sac of Whangkeumbae pear in greenhouse and open field

多核阶段（图3-H），且未检测出单核、二核及四核胚囊。而温室栽培黄金梨胚囊还处于大孢子母细胞减数分裂中，其中单核胚囊（图3-I）、二核胚囊（图3-J）、四核胚囊（图3-K）所占比例分别为27.8%、22.2%、11.1%。此外，在观察开花期胚珠、胚囊切片中发现，温室栽培黄金梨胚囊长度和宽度均小于露地黄金梨（表3），且变异系数大。

结合温室黄金梨胚珠、胚囊发育情况及室内气温发现，正常情况下，在开花前7 d大孢子母细胞开始减数分裂，至开花期胚囊形成。而此时温室内白天平均最高温度高达26.0 ℃，再加上室内高温缩短了现蕾期到开花期的时间，因此，使得温室栽培黄金梨胚囊存在明显的发育滞后现象，到开花期胚囊未发育完全。

表3 温室、露地黄金梨胚珠、胚囊发育情况

Table 3 The development of ovule and embryo sac of Whangkeumbae pear in greenhouse and open field

处理 Treatment	胚珠数 The number of ovule	胚珠大小 The size of ovule/μm				胚囊大小 The size of embryo sac/μm			
		长度 Length	长度变异系数 *CV* of length	宽度 Width	宽度变异系数 *CV* of width	长度 Length	长度变异系数 *CV* of length	宽度 Width	宽度变异系数 *CV* of width
露地 Open field	15	531.7	7.8	264.1	6.4	78.4	7.8	32.9	4.7
温室 Greenhouse	18	384.7	8.6	219.3	6.7	49.2	19.5	21.8	13.0

3 讨 论

胚囊是雌性器官的主要组成部分，胚囊发育不完全或退化容易造成雌性器官不孕。蔡雪等[9]发现花椒胚囊从大孢子母细胞发生到胚囊形成的各个阶段均可发生退化解体，且主要集中在大孢子母细胞减数分裂中期。姚家琳等[10]在研究李胚胎发育过程中发现，在胚囊发育过程中存在着明显的发育滞后现象，导致胚囊形成期结构异常（异性胚囊占比高达67%），珠心珠被提早解体退化，影响授粉受精，从而使得胚胎发育受阻；董军等[11]在杧果胚败育研究中发现，杧果幼胚败育是胚囊在七细胞八核时期助细胞与反足细胞等营养细胞退化，导致授粉受精不良；王近卫等[12]发现珠被、珠孔和胚囊组织形态上的异常是无核白葡萄种子败育的主要原因。笔者通过解剖观察发现，温室栽培黄金梨的胚囊开花期仍有50%处于单核或二核胚囊阶段，11.1%处于四核胚囊阶段，且胚囊的长度和宽度均小于露地。胚囊的发育进度及大小表明，温室栽培黄金梨的胚囊存在明显的发育滞后现象，且滞后比例高达61.1%。拥有发育完全的胚囊是授粉的第一步，温室栽培黄金梨雌性器官不孕是开花期胚囊发育不完全所造成的。

边卫东等[4]和李琛等[5]在对温室甜樱桃坐果率极低的研究中发现，开花前不适宜的高温处理会导致甜樱桃胚珠发育畸形，胚囊败育，这与本试验结果略有不同。由于黄金梨的胚囊发育主要集中在开花前7 d，在结合黄金梨的胚珠发育与温度相关性中发现，开花前的高温处理并不会导致黄金梨胚珠畸形、胚囊败育，而是胚珠正常发育，胚囊发育滞后。关于高温对果树性器官发育不利的影响前人已有多次报道。职倩倩等[13]发现高温会抑制胚珠多糖水解，在加快花芽发育过程中，糖类物质不能满足胚珠、胚囊的快速发育，从而导致胚囊败育。Beppu等[14]研究发现25 ℃以上高温会妨碍白凤桃生殖器官的发育，尤其是胚囊的发育，表现为胚囊发育滞后，坐果率低。在甜樱桃引种试栽及保护地栽培中发现[15-16]，花前25 ℃以上的高温条件会加速胚珠衰老，抑制胚囊发育，表现为甜樱桃的胚囊停留在未发育阶段，并且花后2 d很快退化；姜建福[17]在研究温度对甜樱桃花芽分化的影响过程中，也进一步证实了花期高温会导致甜樱桃胚珠、胚囊败育，从而降低坐果率。

4 结 论

综上所述，温室黄金梨坐果率低、畸形果发生率高的原因应该是开花前不适宜的高温处理缩短了萌芽期到开花期的时间，使得胚囊发育滞后，雌性器官不孕，从而引起种子败育。因此在梨树保护地生产中，为了保证胚囊正常发育，防止种子败育及过多地落果，应适当控制开花前及开花期的温度，尽量使室内温度变化规律接近自然条件下的温度变化规律。

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