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不同授粉品种对‘鸭梨’鸭突及幼果基部内源激素含量的影响

张 莹[1]，刘婉君[1]，成晓华[1]，杜国强[1*]，张玉星[1,2*]

（[1]河北农业大学园艺学院，河北保定 071001；[2]河北农业大学河北省梨工程技术研究中心，河北保定 071001）

摘 要：【目的】研究不同品种花粉授粉对鸭梨幼果基部内源激素水平的影响，探究影响鸭突形成与发育的关键因子。【方法】以30 a（年）生‘鸭梨’（*Pyrus bretschneideri*‘Yali’）为试材，用‘脆梨’‘库尔勒香梨’和‘雪花梨’花粉进行人工授粉，在果实成熟期调查了果实鸭突率和鸭突类型组成，在授粉后10 d、20 d和35 d测定了幼果基部组织内源激素含量。【结果】采用不同梨品种花粉授粉显著影响‘鸭梨’鸭突发生率及鸭突类型组成。以‘脆梨’和‘库尔勒香梨’花粉授粉结实果实的鸭突率分别为100%和84.9%（2016）、99.8%和100%（2017），显著高于以‘雪花梨’花粉授粉结实果实的鸭突率66.7%（2016）和60.7%（2017）；以‘脆梨’花粉授粉结实果实鸭突类型中典型鸭突占比较高，达95.4%（2016）和92.2%（2017），显著高于以‘库尔勒香梨’（54.2%（2016）和63.5%（2017））、‘雪花梨’（46.7%（2016）和50.0%（2017））花粉授粉结实果实典型鸭突率。在幼果发育早期，以‘脆梨’和‘库尔勒香梨’花粉授粉结实的鸭梨幼果基部组织含有相对较高的GA_3、ZR含量，较低的ABA含量，而IAA含量基本无差异；‘脆梨’花粉授粉在提高幼果基部促生长类激素含量和降低ABA含量的效应最强，其次为‘库尔勒香梨’和‘雪花梨’花粉授粉。【结论】不同梨品种花粉授粉影响‘鸭梨’鸭突发生率和鸭突类型组成，鸭突的形成和发育受内源激素调控，幼果基部高水平GA_3和ZR，低水平ABA促进鸭突形成与发育。

关键词：‘鸭梨’；鸭突；形成；发育；授粉品种；内源激素

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Effects of pollinizer cultivars on the morphogenesis and development of Yatu and the endogenous hormone content in the base of young fruit of ‘Yali’ pear (*Pyrus bretschneideri* Rehd.)

ZHANG Ying[1], LIU Wanjun[1], CHENG Xiaohua[1], DU Guoqiang[1*], ZHANG Yuxing[1,2*]

（*[1]College of Horticulture, Hebei Agricultural University, Baoding 071001, Hebei, China; [2]Pear Engineering and Technology Research Center of Hebei Province, Hebei Agricultural University, Baoding 071001, Hebei, China*）

Abstract:【Objective】‘Yali’ (*Pyrus bretschneideri* Rehd.) is native to the Hebei province in China. It is one of the superior traditional pear cultivars. Yatu, formed on the stalk cavity of the fruit, is a typical phenotypic trait of ‘Yali’. The existence and types of Yatu are important indicators for evaluating the quality of pears. Disappearance of Yatu frequently occurs in ‘Yali’ production, and the mechanism is unclear yet. It is important and necessary to clarify the mechanism of Yatu morphogenesis and development. Based on our previous studies, three pollinizer cultivars which had the different influence on Yatu formation were selected to perform controlled pollination for ‘Yali’. This study aimed to explore the factors influencing the morphogenesis and development of Yatu.【Methods】The experiment was carried out from 2016 to 2017 in a commercial pear orchard in Botou, Hebei province, China (38°8′24″ N, 116°31′12″ E). ‘Yali’ trees on *P. betulaefolia* Bunge rootstocks were planted in 1988 with a spacing at 4 m×

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作者简介：张莹，女，在读博士研究生，研究方向：园艺产品质量与安全。Tel：15128488865，E-mail：yingzhang1201@126.com

*通信作者 Author for correspondence. E-mail：gdu@hebau.edu.cn；E-mail：zhyx@hebau.edu.cn

6 m and a north-to-south row orientation. The experiment was designed in a randomized blocks with three replications of two trees each. The first-order flowers within the inflorescence were bagged, and the others within the same inflorescence were removed 2 days before bloom. Then, during bloom, control pollination was performed on the bagged flowers with the prepared pollens of ‘Cuili’, ‘Kuerlexiangli’ and ‘Xuehuali’ pears. The pollen of ‘Cuili’, a native pear variety, was obtained from a local orchard. The pollens of ‘Kuerlexiangli’ pear and ‘Xuehuali’ were obtained from the pear variety preservation garden in Zhaoxian, Hebei province, China. Mature fruit were harvested at 162 days after pollination (DAP). The percentage of fruit with different types of Yatu were counted at 162 DAP. The difference in fruit length between the two opposing sides of a fruit was used as a grading standard for Yatu. One side of the fruit with Yatu was marked by H, and the opposite side was marked by h. The classification of Yatu was determined by the difference between H and h (e.g., H-h). Fruit with a difference greater than 2 mm were identified as the one with Yatu. We classified Yatu into two types based on the value of H-h: small Yatu (2 mm < H-h < 5 mm) and typical Yatu (H-h ⩾5 mm). The distance between the cutting point to the stalk cavity was 1/5 the length of the young fruit, and the base of the fruit was sampled. Samples were collected at 10, 20, and 35 DAP for hormone content determination. Thirty young pear fruit of each treatment were randomly collected, transferred to the lab on ice, sampled as above, ground to powder in liquid nitrogen and stored at −80℃ before being used to measure the hormone content. The hormones were determined by an enzyme-linked immune sorbent assay. The test was replicated three times for each treatment. Three technical replications were run for each biological replication in hormone analysis. The Date Processing System (DPS®) software was used to analyze the data. The significance of differences among means were determined by Duncan’s multiple range test ($p \leqslant 0.05$) using Least Significant Ranges means.【Results】The controlled pollination with different pollination cultivars significantly influenced the percentage and the types of Yatu. With the pollination by ‘Cuili’ and ‘Kuerlexiangli’ pears, the percent of fruit with Yatu was 100%, 84.9% (Year 2016) and 99.8%, 100% (Year 2017), respectively, which was significantly higher than 66.7% (Year 2016) and 60.7% (Year 2017) in pollination with ‘Xuhuali’ pollen. The percent of the typical Yatu in the fruit pollinated by ‘Cuili’ were 95.4% (Year 2016) and 92.2% (Year 2017), which were significantly higher than those pollinated by ‘Kuerlexiangli’ pear [54.2% (Year 2016) and 63.5% (Year 2017)] and ‘Xuehuali’ [46.7% (Year 2016) and 50.0% (Year 2017)]. In the early stage of young fruit development, the fruit pollinated by ‘Cuili’ and ‘Kuerlexiangli’ pear had significantly higher GA_3 and ZR contents, lower ABA content, and less difference in IAA content compared to the fruit pollinated by ‘Xuehuali’. ‘Cuili’ as pollinizer appeared to have the strongest effect to increase the contents of promoting growth hormones and to decrease the content of ABA.【Conclusion】The different pollinizer cultivars influenced the percentage and types of Yatu. The morphogenesis and development of Yatu was regulated by the endogenous hormone balance. The relatively higher GA_3 and ZR content and lower ABA content promoted the morphogenesis and development of Yatu.

Key words: *Pyrus bretschneideri* ‘Yali’; Yatu; Morphogenesis; Development; Pollinizer cultivars; Hormones

‘鸭梨’原产河北，是我国古老的梨主栽优良品种之一[1-2]，因其果形优美、脆而多汁、营养价值高等优点[1]，不仅畅销国内，而且多出口美国、欧盟和东南亚等国家和地区。鸭突是‘鸭梨’的典型特征。‘鸭梨’果实（花托）细胞于芽萌动后开始分裂，花后10 d 处于细胞分裂高峰期，花后约 20 d，果实基部一侧细胞层数相对于另一侧多约 9~10 层，花后 20~25 d 细胞停止分裂，伴随细胞膨大，果实基部细胞

层数多的一侧与果柄连接处凸出于果实表面，形成鸭突[3]。鸭突的有无及类型是评判‘鸭梨’果实外观品质优劣的重要指标之一，近年生产上常出现鸭突不明显的现象，严重影响其商品价值和消费者认可度。

前人研究表明，‘鸭梨’花序序位[4]、光照条件[5]、树体营养[6]、土壤养分[6]、授粉品种[7]和外源生长调节剂[5,8-9]均影响鸭突发育和果形。选用‘面梨’‘胎黄梨’‘脆梨’花粉授粉的‘鸭梨’果实鸭突率均极显著高于‘雪花梨’花粉授粉，前三者之间无显著差异[7]。不同授粉品种影响鸭突形成的机制尚不清楚。外源 GA+BA 可显著提高果实鸭突率，且二者同时使用的促进效果优于单一激素处理[5]；土施 GA 合成抑制剂多效唑（Paclobutrazol, PAC）[8-9]、果实外源涂抹 PAC[5]可显著降低果实鸭突率，表明鸭突的形成受 GA 调控，且 GA 和 BA 在此过程中发挥协同作用。

笔者在前期研究基础上，选择 3 个对鸭突形成影响不同的品种花粉为‘鸭梨’人工授粉，分析其对幼果基部内源激素水平的影响，探讨鸭突形成与发育机制，为有效提高‘鸭梨’鸭突率提供理论依据。

1 材料和方法

1.1 材料

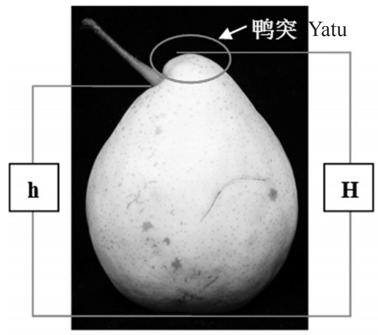
供试梨园位于河北省沧州市泊头亚丰果品有限公司大炉村（38°8′24″ N, 116°31′12″ E），品种为‘鸭梨’，基砧为杜梨，树龄 30 a 生，栽植密度 4 m×6 m。‘雪花梨’和‘库尔勒香梨’花粉采自河北省石家庄赵县梨品种保存园，‘脆梨’花粉采自大炉村果园。

1.2 试验设计与处理

分别于 2016 和 2017 年气球期采集‘脆梨’‘库尔勒香梨’和‘雪花梨’花蕾，剥取花药，在 25 ℃自然散粉后置于−20 ℃保存备用。于‘鸭梨’开花前 2 d 对花序 1 序位花套授粉袋，同时疏除同花序其他序位花，于开花当天用上述 3 个品种花粉对 1 序位花进行人工授粉，授粉后套袋，10 d 后摘袋，随机区组设计，每小区 2 株，3 次重复。于授粉后 162 d，即‘鸭梨’果实成熟期，调查经不同品种花粉授粉果实的鸭突率和鸭突类型组成。于授粉后 10、20 和 35 d，切取幼果基部组织（果实基部横切线与果实基部最高点的距离为全果纵径的 1/5），经液氮速冻后于超低温保存，用于激素含量测定。每处理随机采集花序 1 序位果实共 30 个，3 次重复。

1.3 鸭突类型划分标准

用游标卡尺测量高度。果实具鸭突一侧高度为 H，其对侧为 h（图 1），鸭突高度为 H-h。H-h>2 mm，表示果实形成了鸭突。根据鸭突高度划分鸭突类型，当 2 mm < H-h < 5 mm 时，为小型鸭突；当 H-h > 5 mm 时，为典型鸭突。



图中果实基部被红线圈起的部分为鸭突，果实具鸭突一侧及其对侧高度分别用 H 和 h 表示，鸭突高度为 H-h。

Yatu, which is circled by the red oval, on the base of the fruit were well developed. The lengths of the right and left side of the fruit fare indicated by H and h, respectively. The classification of Yatu was determined by the difference between H-h.

图1 鸭突表型及其高度测量方法

Fig. 1 The phenotype and the measuring method of Yatu

1.4 果实内源激素提取及含量测定方法

将样品在液氮中充分研磨至粉末状后，迅速称取 0.2 g 置于 10 mL 离心管中，加入 8 mL 预冷 80% 甲醇，超声波震荡提取 1 h，置于 4 ℃避光浸提 12 h 后于 4 ℃ 12 000 r·min^{-1} 离心 15 min，将上清液转移至 10 mL 离心管中，氮气吹至管内剩余 1.5~2.0 mL 液体，用磷酸氢二钾调节 pH 至 8.0，加入 0.2 g PVPP 除杂，超声波震荡 30 min，4 ℃ 12 000 r·min^{-1} 离心 5 min，转移上清液至新的离心管中，调节 pH 至 3.0，加入 3 mL 乙酸乙酯萃取，超声波震荡 10 min，静置 2 h，转移上层有机相并用氮气吹干，加入 2 mL 20%甲醇复溶后通过已活化的 C18 小柱，再用 2 mL 10%甲醇淋洗，弃除流出液。用 1 mol·L^{-1} NaOH 调节甲醇 pH 至 8.0，用 1 mL pH 8.0 的甲醇冲洗 C18 小柱即得样品提取液。样品测定采用酶标法，参照 Yang 等[10]的方法进行，测定过程依次为包被、洗板、竞争、洗板、加二抗、洗板、加底物显色和比色。

1.5　数据分析

利用DPS软件进行数据统计与分析。

2　结果与分析

2.1　不同品种花粉授粉对鸭突形成和鸭突类型组成的影响

分别以‘脆梨’‘库尔勒香梨’和‘雪花梨’花粉对‘鸭梨’进行授粉，于果实成熟期调查果实鸭突发生情况，结果如表1所示，以‘脆梨’花粉授粉的‘鸭梨’果实中鸭突率最高，达到100%（2016年）和99.8%（2017年），其次为以‘库尔勒香梨’花粉授粉的果实，两者均显著高于以‘雪花梨’花粉授粉的果实。将鸭突分为典型鸭突和小型鸭突两种类型，发现以‘脆梨’花粉授粉的‘鸭梨’果实中典型鸭突率为95.4%（2016年）和92.2%（2017年），显著高于以‘库尔勒香梨’‘雪花梨’花粉授粉的果实典型鸭突率。表明‘脆梨’和‘库尔勒香梨’花粉授粉均可显著提高‘鸭梨’果实鸭突发生率，但影响程度存在差异，‘脆梨’花粉授粉可显著提高典型鸭突率，效应显著优于‘库尔勒香梨’花粉授粉。

表1　不同品种花粉授粉的‘鸭梨’果实鸭突率和鸭突类型

Table 1　The percentage of ‘Yali’ pear fruit with Yatu and the formation of different types of Yatu after pollinating with different pear cultivars

年份 Year	授粉品种 Pollinizer cultivar	鸭突率 The percentage of fruits with Yatu/%	不同类型鸭突百分率 The percentage of fruits with different types of Yatu/%	
		H-h > 2 mm	小型鸭突 Small Yatu 2 mm < H-h < 5 mm	典型鸭突 Typical Yatu H-h > 5 mm
2016	雪花梨 Xuehuali	66.7±2.5 c	20.0±1.6 b	46.7±3.6 b
	库尔勒香梨 Kuerlexiangli	84.9±2.3 b	30.7±1.2 a	54.2±1.6 b
	脆梨 Cuili	100.0±0.0 a	4.6±0.3 c	95.4±2.3 a
2017	雪花梨 Xuehuali	60.7±3.6 b	10.7±1.5 b	50.0±7.4 b
	库尔勒香梨 Kuerlexiangli	100.0±0.0 a	36.5±2.0 a	63.5±7.7 b
	脆梨 Cuili	99.8±0.2 a	7.6±0.6 c	92.2±2.1 a

注：表中同列数据后不同小写字母表示在0.05水平上差异显著。

Note: The different small letters following the value in the same column indicate significant difference at $p < 0.05$.

2.2　不同品种花粉授粉对幼果基部组织内源激素含量的影响

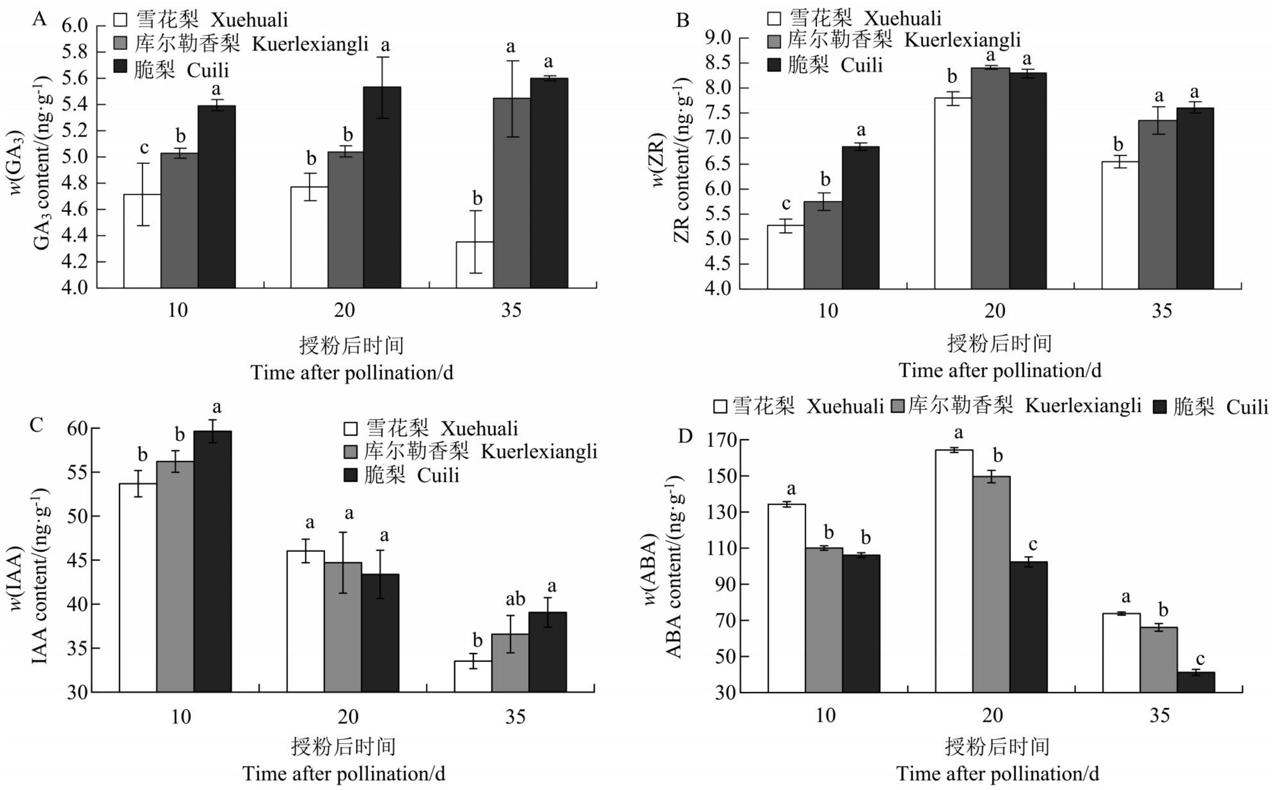
授粉后10 d，经‘脆梨’‘库尔勒香梨’和‘雪花梨’花粉授粉的‘鸭梨’幼果基部组织中GA_3、ZR、IAA和ABA含量表现不同程度差异。其中GA_3、ZR和IAA含量，以‘脆梨’花粉授粉的幼果最高，‘雪花梨’花粉授粉的幼果最低；ABA含量则表现为以‘雪花梨’花粉授粉的幼果显著高于以‘脆梨’和‘库尔勒香梨’花粉授粉的幼果（图2）。

授粉后20 d，以‘脆梨’花粉授粉的幼果仍保持相对较高的GA_3含量和较低的ABA含量；其ZR含量与以‘库尔勒香梨’花粉授粉幼果无显著差异，但二者均显著高于‘雪花梨’花粉授粉的幼果；所有处理的幼果IAA含量无显著差异。

授粉后35 d，以‘脆梨’和‘库尔勒香梨’花粉授粉幼果GA_3和ZR含量无差异，均显著高于‘雪花梨’花粉授粉的幼果；所有处理的幼果IAA含量差异不明显；处理间ABA含量均呈差异显著，以‘脆梨’花粉授粉幼果含量最低，‘雪花梨’花粉授粉的幼果含量最高。

2.3　不同品种花粉授粉对幼果基部组织中内源激素含量比例的影响

授粉后10 d、20 d和35 d不同品种花粉授粉结实的‘鸭梨’幼果基部组织中促长激素GA_3、ZR、IAA和抑长激素ABA含量比呈现规律性变化，除在授粉后20 d‘库尔勒香梨’与‘雪花梨’花粉授粉结实幼果基部IAA/ABA无显著差异外（图3-C），其余处理间同时期GA_3/ABA、ZR/ABA和IAA/ABA均表现显著差异，其中以‘脆梨’花粉授粉幼果促长激素与抑长激素比值最高，依序分别为以‘库尔勒香梨’和‘雪花梨’花粉授粉结实幼果（图3）。



同一时间点处理柱状图上不同字母表示在 0.05 水平上差异显著。下同。

Different letters above the bars at the same time indicate significant difference at $p < 0.05$ among treatments. The same below.

图2 不同梨品种花粉授粉对'鸭梨'幼果基部内源激素含量的影响

Fig. 2 Effects of pollinizer cultivars on endogenous hormone content at the base of young fruit of 'Yali' pear

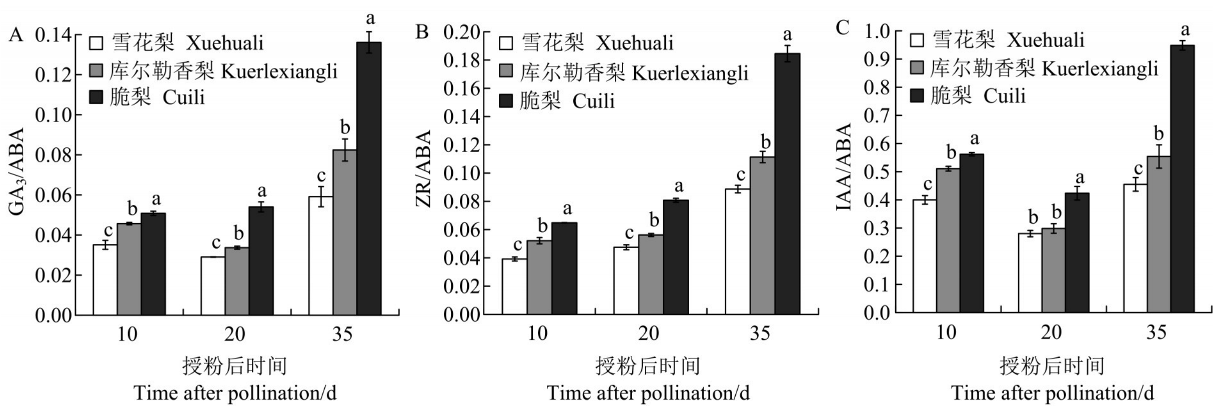


图3 不同梨品种花粉授粉对'鸭梨'幼果基部组织中激素比例的影响

Fig. 3 Effects of pollinizer cultivars on the proportion between plant hormone at the base of young fruit of 'Yali' pear

3 讨 论

作为'鸭梨'典型特征的鸭突性状常因授粉品种的不同而表现差异。本研究发现'脆梨'花粉授粉可显著提高果实鸭突发生率和典型鸭突率，促进了鸭突的发生和发育；'库尔勒香梨'花粉授粉提高了果实鸭突发生率，即促进了鸭突的发生，但产生的鸭突中多为小鸭突，典型鸭突率与'雪花梨'授粉无显著差异，因而对鸭突发育影响相对不明显。表明'脆梨'和'库尔勒香梨'花粉授粉对鸭突发育的影响程度不同。前人关于不同授粉品种影响'鸭梨'果实鸭突形成与发育的研究较少，董存田等[7]的

研究发现，‘面梨’‘胎黄梨’‘脆梨’花粉授粉‘鸭梨’果实鸭突率显著高于‘雪花梨’花粉授粉，三者之间无显著差异，但并未研究不同授粉品种对鸭突发育的影响程度。本研究依据鸭突高度将其划分为小型鸭突和典型鸭突，结合不同授粉品种对鸭突类型组成的影响和鸭突发育关键时期幼果基部内源激素含量和比例差异，认为幼果基部高水平 GA_3 和 ZR，低水平 ABA 促进鸭突发生；授粉品种在提高幼果基部 GA_3 和 ZR 含量，降低 ABA 含量的效应强，对鸭突发育的促进效果明显，形成典型鸭突的数量多。在‘鸭梨’生产中可将其作为参考以调控鸭突形成与发育。

徐胜利等[11]和 Denny[12]认为，不同品种花粉授粉后果实内源激素水平差异调控果实发育并引起果实表型差异。植物激素参与调控果实细胞分裂与膨大[13]，激素水平和各激素间的协同或拮抗作用共同调控果实发育[14]。细胞分裂素作为细胞分裂的诱导因子，在果实发育过程中对细胞分裂起激发和促进作用[15-16]，并可通过调运同化产物的运输促进细胞膨大[17]；GA 可促进细胞纵向伸长，GA_3 也可通过缩短细胞分裂周期加速细胞分裂[18-19]。本研究分析不同品种授粉的‘鸭梨’幼果基部内源激素水平差异，发现鸭突的形成和发育受内源激素调控。幼果基部高水平 GA_3 和 ZR，低水平 ABA 促进细胞分裂，提高了果实库强，增强调运同化产物能力，促进细胞膨大，为鸭突形成与发育奠定基础。

傅玉瑚等[5]在‘鸭梨’幼果基部涂抹 GA+BA 显著促进鸭突膨大，提高果实鸭突率。在本研究中，幼果基部高水平 GA_3 和 ZR 促进鸭突形成和发育，表明 GA_3 和 ZR 在促进鸭突形成与发育过程中发挥协同作用，在鸭突部位细胞旺盛分裂时期，通过协同促进此部位细胞分裂与膨大促进鸭突发育。ABA 可抑制细胞伸长和植物生长，其对果实的生长发挥“制动”平衡作用[20]。有研究表明，促生长类激素和抑制生长类激素的平衡关系对果实发育至关重要[21-22]。在甜橙果实细胞分裂和膨大期，大果锦橙中 IAA/ABA 和 GA_3/ABA 大于长叶锦橙，为大果锦橙果实大于长叶锦橙的原因之一[23]。本研究中，‘脆梨’花粉授粉结实幼果基部较高的 GA_3/ABA、ZR/ABA 和 IAA/ABA 提高了鸭突发生数量和典型鸭突数量，促进了鸭突形成与发育，结果表现一致。

4 结　论

不同梨品种花粉授粉影响‘鸭梨’鸭突发生率和鸭突类型组成，‘脆梨’和‘库尔勒香梨’花粉授粉均可显著促进鸭突形成，其中‘脆梨’花粉授粉对典型鸭突形成的促进效果优于‘库尔勒香梨’花粉授粉。‘脆梨’花粉授粉在提高幼果基部促生长类激素含量和降低 ABA 含量的效应最强，其次为‘库尔勒香梨’和‘雪花梨’，鸭突的形成和发育受内源激素调控，幼果基部高水平 GA_3 和 ZR，低水平 ABA 促进鸭突形成与发育。

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