

利用 *PSY* 基因标记探讨枇杷果肉颜色的遗传倾向

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摘要:【目的】研究枇杷果肉颜色的遗传倾向。【方法】以黄肉品种‘梅花霞’和‘早钟6号’及白肉品种‘白玉’为亲本, 创建了9个杂交和自交后代群体, 利用SRAP和RAPD分子标记技术, 鉴定真杂种。利用枇杷果实特异DNA分子标记*PSY*基因对9个杂交和自交组合后代的果肉颜色进行早期鉴定, 并对其遗传倾向进行分析。【结果】9个杂交和自交后代群体中, 共鉴定出1 166株真杂种。‘梅花霞’与‘白玉’和‘梅花霞’与‘早钟6号’的正反交组合后代未出现果肉颜色性状的分离倾向, 果肉颜色均鉴定为黄色; 而‘早钟6号’与‘白玉’的正反交组合后代果肉黄、白色的分离比分别为1:0.89和1:0.87。自交组合‘梅花霞’和‘白玉’的后代无果肉颜色性状的分离, 后代果肉颜色分别鉴定为黄色和白色; 而‘早钟6号’自交后代黄肉与白肉分离比例为2.94:1。【结论】枇杷果肉颜色黄色和白色可能受到一对呈显隐关系的基因控制, 其中黄肉性状为显性, 存在纯合和杂合的情况, 其分子标记类型不同, DNA分子标记分别表现为1 031 bp(纯合)或1 031 bp和319 bp(杂合); 白肉性状为隐性, DNA分子标记为319 bp。

关键词: 枇杷; 果肉颜色; 分子标记; *PSY*基因; 遗传倾向

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Study on the inheritance of fruit color in loquat based on *PSY* gene marker

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Abstract:【Objective】Loquat (*Eriobotrya japonica* Lindl.), a genus of flowering plants in the *Rosaceae* family, has been cultivated in China more than 2 000 years. The carotenoid is the main pigment in loquat fruit, which leads to a difference in flesh color. Traditionally, loquat cultivars can be divided into two groups based on its flesh colors, that is, yellow-flesh and white-flesh. Compared with yellow-flesh cultivars, white-fleshed cultivars have become more popular because of their delicious flesh and higher economic value, and breeders also prefer to breed new white-flesh cultivars. However, the genetic mechanism of loquat flesh color is still unclear. Loquat breeding is limited at the seedling selection stage because of the long juvenile period. Therefore, it is very important to study the genetic inheritance of loquat flesh color. In this study, we analyzed the flesh color segregation ratio of different crossing combinations in order to study the genetic inheritance of loquat flesh color. Flesh color specific molecular markers were used to identify the flesh color of hybrid progenies at seedling stage.【Methods】Based on the specific molecular markers of loquat flesh color, there are two types of molecular markers in yellow-flesh loquat cultivars: some yellow-flesh cultivars possess a long amplified fragment (1 013 bp), some possess two amplified fragment: a long fragment (1 013 bp) and a short fragment (319 bp). However,

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all white-flesh cultivars possess only a short amplified fragment (319 bp). Therefore, two types of yellow-flesh cultivars ‘Meihuaxia’ and ‘Zaozhong No. 6’ and one white-flesh cultivar ‘Baiyu’ were selected as parent materials in this study. Field crossing and selfing were carried out in 2017, and a total of 9 progeny populations were created, including 6 cross combinations and 3 selfing combinations. Among these progeny populations, the largest combination was ‘Baiyu’ × ‘Meihuaxia’, the number of offsprings were 153; the small estprogeny came from the selfing of ‘Meihuaxia’, the number of offsprings were 110. After sowing and seedling, the genomic DNA of each single plant of the 9 hybrid combinations was extracted and the RAPD and SRAP molecular markers were used to identify the true and false hybrids of the offspring. We found that 10 RAPD primers, 9 SRAP forward primers and 11 reverse primers could be used for further identification. Altogether 1166 offspring individuals were screened as true hybrids by RAPD and SRAP molecular markers and the average true hybrid rate was 91.35%. The flesh color of each offspring of 9 progeny populations was identified using loquat flesh color specific DNA molecular markers at seedling stage, and their genetic inheritance was also investigated. Chi-square test was used to test whether the separation ratio of flesh color was in accordance with Mendelian’s law of heredity.【Results】The fruit flesh color segregation rations were different in different hybrid combinations. The hybrid combinations ‘Meihuaxia’ × ‘Baiyu’ and ‘Baiyu’ × ‘Meihuaxia’ did not show segregation in flesh color, the flesh color of their offsprings were all identified as yellow. The same results appeared in the hybrid combinations ‘Meihuaxia’ × ‘Zaozhong No. 6’ and ‘Zaozhong No. 6’ × ‘Meihuaxia’, their offsprings were all identified as yellow-flesh. However, the flesh color was obviously separated in the hybrid combination of ‘Zaozhong No. 6’ × ‘Baiyu’ and ‘Baiyu’ × ‘Zaozhong No. 6’, the separation ratios of yellow flesh and white flesh were 1:0.89 and 1:0.87, respectively. Their separation ratio was in accordance with Mendelian's law of heredity. In the three selfing progenies of ‘Meihuaxia’ and ‘Baiyu’ there was no segregation on fruit flesh color, all offsprings of ‘Meihuaxia’ selfing were identified as yellow-flesh and all offsprings of ‘Baiyu’ selfing were identified as white-flesh. But, in selfing progeny of ‘Zaozhong No.6’, the segregation ratio of yellow and white flesh was 2.94:1, and its separation ratio was also in accordance with Mendelian’s law of heredity.【Conclusion】For the first time, we used specific DNA molecular markers to study the separation of loquat flesh color from 9 different hybrid combinations. Our results showed that loquat flesh color was controlled by a pair of allele. The yellow flesh trait was dominant and white flesh trait was recessive. By the way, we could further distinguish the homozygous or heterozygous state of loquat yellow flesh trait using specific DNA molecular markers, the genotype of yellow-flesh was homozygous when the amplified band was a single long fragment (1 013 bp) and the DNA molecular markers were two amplified fragments (1 013 bp and 319 bp). The genotype of yellow-flesh was heterozygous. These results can provide a theoretical basis for the breeding of new loquat cultivars, especially for the breeding of the new white-flesh loquat cultivars.

Key words: Loquat; Flesh color; Molecular markers; *PSY*; Genetic inheritance

枇杷(*Erobotrya Japonic* Lindl.)原产于中国,已有 2 000 多年的栽培历史,是我国重要的早春水果之一。我国枇杷的栽培面积和总产量均居世界第一^[1],主要栽培区集中在长江流域及其以南各省^[2],其中四川、福建和浙江的栽培面积较大,先后成为我国枇杷行业的领跑者^[3]。20 世纪 90 年代,黄金

松等^[4]首先报道了利用杂交育种技术育成了中国首个杂交枇杷品种‘早钟 6 号’,并由此建立了枇杷有性杂交育种技术体系,而杂交育种也成为枇杷新品种选育的有效手段。因此,开展枇杷的性状遗传规律研究,可为杂交亲本的选配及后代选择提供理论依据。

枇杷果实的颜色是一个重要经济性状,依据果肉颜色的不同,大致可分为两类:白肉枇杷和黄肉枇杷。白肉枇杷因具有肉质细腻、清甜、风味浓郁、汁多味甜等特点,越来越受到消费者欢迎,育种家也更加重视白肉枇杷的育种,因此,研究枇杷果实颜色性状的遗传倾向显得十分重要。分子标记辅助育种(MAS)可以缩短育种周期和提高育种效率,广泛应用于许多作物^[5-7]。目前,DNA 标记广泛用于枇杷各项研究,如评估遗传多样性^[6-9],遗传连锁图谱^[10-12]和种质鉴定^[13-14];而对枇杷果实颜色的分子标记研究较少^[15],利用枇杷白肉品种为研究材料,获得的部分特异标记可以区分‘贵妃’、‘新白1号’和‘新白8号’^[16]。

2016年,本课题组发现利用 *PSY* 基因在黄、白肉枇杷品种中的差异^[17],经过扩大群体验证,可以准确地区分黄、白肉枇杷品种,不同黄肉枇杷品种中有两种不同扩增类型,一种类型可扩增出两条片段(1 013 bp 和 319 bp),另一种是只能扩增一条片段(1 013 bp),而所有的白肉枇杷品种中只能扩增出一条片段(319 bp)^[18],为进一步研究枇杷果实颜色的遗传规律奠定了基础。笔者以黄肉品种‘早钟6号’、‘梅花霞’和白肉品种‘白玉’为亲本材料,创制杂交后代群体,并利用已获得的枇杷果肉颜色特异分子标记对杂种后代个体果实颜色进行了早期鉴定,同时对其遗传倾向进行分析,旨在探索枇杷果实颜色性状的遗传规律,为白肉枇杷新品种杂交育种亲本的选配和杂种后代选择提供参考依据。

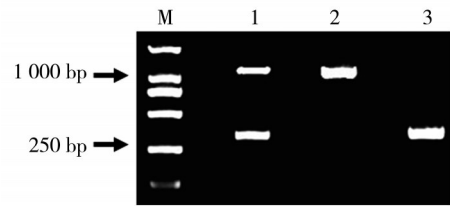
1 材料和方法

1.1 亲本的选择与选配

利用枇杷果实颜色特异的分子标记,选择两种类型的黄肉品种‘梅花霞’、‘早钟6号’和白肉品种‘白玉’进行正反交和自交,创建了9个杂交(自交)群体(1 166株),分别是:‘梅花霞’×‘白玉’、‘白玉’×‘梅花霞’、‘早钟6号’×‘白玉’、‘白玉’×‘早钟6号’、‘梅花霞’×‘早钟6号’、‘早钟6号’×‘梅花霞’、‘梅花霞’⊗、‘白玉’⊗、‘早钟6号’⊗。所有材料均取自于华南农业大学枇杷种质资源圃(广东广州)(图1)。

1.2 方法

1.2.1 田间杂交 2017—2018年创制了杂交(自交)群体,田间杂交的工作如下:杂交选取枇杷盛花期含苞待放的花蕾,每穗留8~10枚花朵,小心去除雄蕊,将收集的父本花粉授在母本花朵的柱头上,



M. Marker; 1. 早钟6号; 2. 梅花霞; 3. 白玉。

M. Marker; 1. Zaozhong No. 6; 2. Meihuaxia; 3. Baiyu.

图1 所选亲本特异PCR扩增式样

Fig. 1 Electrophoretic amplification profile of selected parents

授粉后立即用双层纸袋隔离,待坐果稳定后去掉外层纸袋,保留内层纸袋直至果实成熟。田间杂交工作在华南农业大学枇杷种质资源圃完成。第二年春果实成熟时,收获种子,种子清洗后播种,每个杂交群体单独播种,获得杂种苗。

1.2.2 真假杂种鉴定 利用两种分子标记(SRAP和RAPD)技术,对9个组合的实生后代进行了真假杂种的鉴定,方法主要参考乔燕春等^[19]和付燕^[20]的方法。经过3次重复,筛选获得可用于真假杂种鉴定的SRAP分子标记正向引物9条,反向引物11条,RAPD分子标记引物10条。引物筛选好后,对杂交后代进行鉴定,PCR扩增产物在2.0%琼脂糖、5 V·cm⁻¹电压下电泳。电泳结果比较杂交后代中带有父本特异清晰条带,判断为真杂种。

1.2.3 特异PCR扩增 果实颜色特异分子标记扩增体系和PCR程序参照文献[18],体系见表1。

扩增体系反应程序:94℃预变性5 min,94℃变性30 s,55℃复性30 s,72℃延伸1 min,35个循环,72℃后延伸5 min,4℃保存。1.5%琼脂糖电泳检测PCR产物。

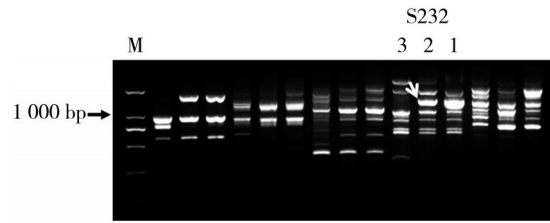
表1 枇杷果实颜色特异分子标记扩增体系
Table 1 Specific-PCR system for loquat color

反应组分 Reaction component	组分量 Content/ μ L
Taq Mix	10
DNA 模板(50 ng·mL ⁻¹)	2
DNA temple (50 ng·mL ⁻¹)	
引物1(10 μ mol·L ⁻¹)	0.5
Primer1(10 μ mol·L ⁻¹)	
引物2(10 μ mol·L ⁻¹)	0.5
Primer2(10 μ mol·L ⁻¹)	
双蒸水	7
ddH ₂ O	

2 结果与分析

2.1 真假杂种引物的筛选

利用 RAPD 和 SRAP 分子标记技术对杂交后代进行真假杂种的鉴定结果表明,在 RAPD-PCR 反应中,引物 S232(1 500 bp 左右)可作为‘白玉’×‘梅花霞’、‘白玉’×‘早钟 6 号’的杂种鉴定(图 2);而在 SRAP-PCR 反应中,引物 me2em3(1 000 bp 左右)可作为‘梅花霞’×‘早钟 6 号’的杂种鉴定;引物 me6em6(750 bp 左右)可作为‘梅花霞’×‘白玉’的杂种鉴定;引物 me8em5(2 000 bp 左右)可作为‘早钟 6 号’×‘白玉’的杂种鉴定;引物 me2em5(1 000 bp 左右)可作为‘早钟 6 号’×‘梅花霞’的杂种鉴定(图 3)。



M. Marker; S232.RAPD 引物; 1. 早钟 6 号; 2. 梅花霞; 3. 白玉; 箭头示亲本中特异条带。

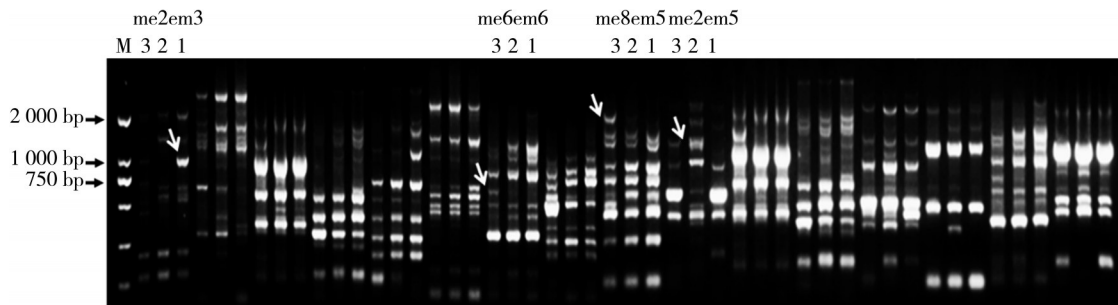
M. Marker; S232. RAPD primers; 1. Zaozhong No.6; 2. Meihuaxia; 3. Baiyu; Arrow means specific band of parents.

图 2 RAPD 分子标记引物的筛选

Fig. 2 Primer screening for RAPD

2.2 杂交后代群体真杂种率

从表 2 可以看出,各组合的真杂种率存在差异,其中组合‘白玉’×‘早钟 6 号’获得了最高的真杂种率



M. Marker; me2em3, me6em6, me8em5 和 me2em5. SRAP 引物; 1. 早钟 6 号; 2. 梅花霞; 3. 白玉; 箭头示亲本中特异条带。

M. Marker; me2em3, me6em6, me8em5 and me2em5. SRAP primers; 1. Zaozhong No.6; 2. Meihuaxia; 3. Baiyu; arrows mean specific bands of parents.

图 3 SRAP 分子标记引物的筛选

Fig. 3 Primer screening for SRAP

率,为 93.75%,而组合‘早钟 6 号’×‘梅花霞’的真杂种率最低,为 85.91%。

2.3 杂交后代群体果实颜色的分离情况

由图 4 可知,杂交组合‘梅花霞’×‘白玉’和‘白玉’×‘梅花霞’后代分子标记类型相同,均为两条扩增片段(1 013 bp 和 319 bp),表明后代未出现果实

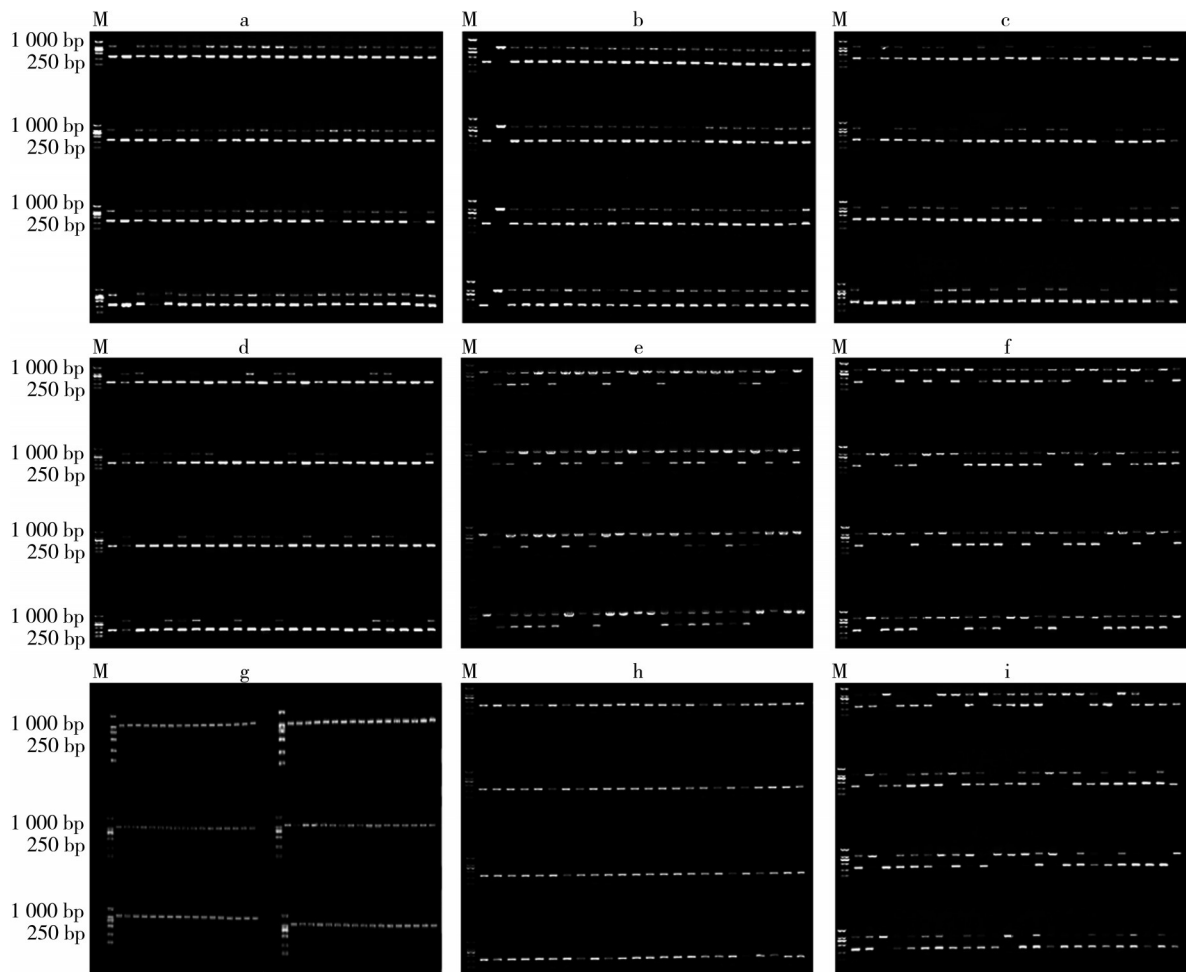
表 2 9 个杂交(自交)组合后代真杂种率

Table 2 True hybrid rate of 9 cross (self-crossed) combinations

亲本组合 Combination	F ₁ 代总株数 No. of F ₁	F ₁ 代真杂种种数 No. of true hybrids	真杂种率 True hybrid rate/%
梅花霞×白玉 Meihuaxia × Baiyu	124	112	90.63
白玉×梅花霞 Baiyu × Meihuaxia	153	140	91.80
早钟 6 号×白玉 Zaozhong No. 6 × Baiyu	147	136	92.78
白玉×早钟 6 号 Baiyu × Zaozhong No. 6	150	140	93.75
梅花霞×早钟 6 号 Meihuaxia × Zaozhong No. 6	129	120	93.25
早钟 6 号×梅花霞 Zaozhong No. 6 × Meihuaxia	138	118	85.91
梅花霞自交 Meihuaxia	110	110	*
白玉自交 Baiyu	140	140	*
早钟 6 号自交 Zaozhong No. 6	150	150	*

注:*默认 100%真杂种率。

Note: * means 100% hybrid.



M. Marker; a. 梅花霞×白玉; b. 白玉×梅花霞; c. 早钟6号×白玉; d. 白玉×早钟6号; e. 梅花霞×早钟6号; f. 早钟6号×梅花霞; g. 梅花霞 ⊗; h. 白玉 ⊗; i. 早钟6号 ⊗。

M. Marker; a. Meihuaxia × Baiyu; b. Baiyu × Meihuaxia; c. Zaozhong No.6 × Baiyu; d. Baiyu × Zaozhong No.6; e. Meihuaxia × Zaozhong No.6; f. Zaozhong No.6 × Meihuaxia; g. Meihuaxia; h. Baiyu; i. Zaozhong No.6.

图4 9个杂交(自交)组合后代特异PCR扩增图谱

Fig. 4 Specific PCR amplification profile for 9 cross (self-crossed) combinations

颜色性状的分离,果肉颜色全部表现为黄肉;杂交组合‘早钟6号’×‘白玉’和‘白玉’×‘早钟6号’后代出现两种分子标记类型,分别是1 013 bp和319 bp或319 bp,说明果肉颜色性状产生了分离,经统计枇杷果肉黄、白色的分离比分别为1:0.89和1:0.87,卡方检验(表3)表明遗传分离比符合孟德尔遗传定律;在杂交组合‘梅花霞’×‘早钟6号’和‘早钟6号’×‘梅花霞’中,杂交后代分子标记类型不同,表现为两种分子标记类型(1 013 bp和319 bp或1 013 bp),表明后代个体果实为黄肉类型。

在3个自交组合中,自交组合‘梅花霞’的后代分子标记类型相同,均为单一的扩增片段(1 013 bp),说明果肉颜色性状没有发生分离,全部表现为黄色;同样,‘白玉’的自交后代分子标记类型相同,

为一条扩增片段(319 bp),说明果肉颜色性状没有发生分离并且均表现为白色;而‘早钟6号’自交群体后代出现了三种分子标记类型,分别为1 013 bp(26%)、1 013 bp和319 bp(49%)、319 bp(25%),其果肉颜色分离比例为2.94:1,卡方检验表明其分离符合孟德尔遗传定律。卡方测验^[21]结果表明本实验结果所测得的数据均小于理论推测值,说明本试验数据可靠。

3 讨论

杂交育种是指利用杂交技术将不同亲本上的优良性状组合到杂种中,并对其进行选择,从而获得新品种的过程^[22]。果树性状主要包括主基因控制的质量性状和多基因控制的数量性状两大类,但果树

表3 9个杂交(自交)后代群体分离比及卡方测验
Table 3 Separation ratio and χ^2 test of 9 cross (self-crossed) combinations

亲本组合 Combination	F ₁ 代分子标记类型 DNA marker of F ₁			黄白肉分离比 Separation ratio of yellow-and white-flesh	χ^2
	1 013 bp/319 bp	1 013 bp	319 bp		
梅花霞×白玉 Meihuaxia × Baiyu	112.00	0.00	0.00	0.00	0.00
白玉×梅花霞 Baiyu × Meihuaxia	140.00	0.00	0.00	0.00	0.00
早钟6号×白玉 Zaozhong No. 6 × Baiyu	72.00	0.00	64.00	1:0.89	0.53
白玉×早钟6号 Baiyu × Zaozhong No. 6	75.00	0.00	65.00	1:0.87	0.71
梅花霞×早钟6号 Meihuaxia × Zaozhong No. 6	56.00	64.00	0.00	0.00	0.00
早钟6号×梅花霞 Zaozhong No. 6 × Meihuaxia	63.00	55.00	0.00	0.00	0.00
梅花霞自交 Meihuaxia	0.00	110.00	0.00	0.00	0.00
白玉自交 Baiyu	0.00	0.00	140.00	0.00	0.00
早钟6号自交 Zaozhong No.6	72.00	40.00	38.00	2.95:1	0.01

往往存在生长周期长和遗传背景复杂的现象,所以其性状的遗传方式也比较复杂^[23]。

果实颜色是果树育种的重要的经济性状,不同的树种果实颜色的遗传规律不相同。王宇霖^[24]对49个杂交组合的梨杂种后代进行亲本性状的遗传倾向进行了研究,结果发现梨的果皮色泽红绿对褐色或褐绿为显性。俞明亮^[25]利用杂交手段研究桃果肉颜色遗传倾向探究,发现白色果肉对红色果肉为完全显性;而同样在桃上,不同的杂交组合中发现红肉性状在所有试验组合中均呈显性,后代群体红肉桃单株与白肉桃单株比例接近1:1,符合一对等位基因分离规律^[26-27]。在葡萄上利用‘红地球’红肉葡萄与白肉葡萄进行杂交,发现后代葡萄果皮颜色出现性状分离,且分离比(白色:红色)接近1:3,但经卡平方分类验证,并不是所有类型都符合遗传比率规律,认为控制葡萄果皮颜色不只是由1对显隐基因控制^[28]。

与这些果树种类相比,涉及枇杷性状遗传研究相对较少,郑少泉等^[29-30]对枇杷早实性、成熟期、叶片抗病性及果实的果重、果形、皮色、肉色等性状进行了研究,认为果实颜色遗传是按复杂的图式进行的,可能是由一对或多对基因控制的不完全显性遗传。宋红彦等^[3]分析了4个杂交组合后代果实的颜色的分离情况提出:由试验结果看,尽管杂交双亲都属于黄肉枇杷,但是在杂交后代出现了相当部分的白肉枇杷单株,初步看来似乎是黄肉对白肉为3:1的分离比,白肉似乎为隐性性状,受隐性基因控制的,但需要进一步的严格试验加以验证。谢丽雪等^[31]年以‘早钟6号’为母本,‘贵妃’为父本进行

了杂交工作,连续三年的调查发现已结果的后代56株个体中,其中果实为黄肉个体有26株,果实为白肉的个体有30个,二者比例接近1:1。笔者以2个不同类型的黄肉枇杷品种和1个白肉品种为亲本,创制了9个杂交(自交)组合,利用已获得的枇杷果实颜色的特异分子标记,对不同组合的1166个后代个体果实的颜色进行了早期鉴定,并对其遗传倾向进行了研究,结果表明,枇杷果实颜色可能受到一对呈显隐关系的基因控制,其中黄肉性状为显性,白肉性状为隐性;同时,针对于果实的颜色,在黄肉枇杷品种中存在基因呈显性纯合或杂合类型,其基因型可记为AA或Aa,而白肉枇杷品种基因型为aa,这个研究结果与前人研究结果相同^[32];而与之不同的是,我们利用特异的DNA分子标记,可进一步区分枇杷黄肉性状基因纯合或杂合状态,其中基因型为AA时,其DNA分子标记为单一扩增条带(1013 bp);基因型为Aa时,其DNA分子标记为两条扩增条带(1013 bp和319 bp),这个研究结果为杂交亲本的选择与选配,特别是为白肉枇杷新品种选育提供了理论依据。

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