

‘串枝红’×‘骆驼黄’杏F₁代糖酸性状的遗传变异分析

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摘要:【目的】探索杏F₁代群体果实糖酸性状的遗传变异规律,为科学选配亲本提供理论支持。【方法】以杏品种‘串枝红’和‘骆驼黄’为亲本进行杂交,亲本及F₁代群体果实中蔗糖、葡萄糖和果糖含量采用离子色谱测定,苹果酸和柠檬酸含量采用高效液相色谱(HPLC)测定。【结果】杂交后代果实中可溶性糖以蔗糖为主,含量(ω ,后同)范围为43.55~100.85 mg·g⁻¹。糖酸组分(除柠檬酸)、总糖和总酸含量均呈正态分布,说明它们是多基因控制的数量性状,而柠檬酸含量主要集中在低酸区域,表现为偏正态分布,表明其遗传可能存在主效基因。各糖酸组分含量在杂交后代中均出现广泛分离(变异系数均超过20%),后代酸含量的变异系数均高于糖,表明糖比酸的选择潜力更大。杂交后代蔗糖、柠檬酸和总酸含量低于亲中值,表现为衰退变异。杂交后代糖酸性状的广义遗传力(H^2)差异不明显,均在0.70以上,其中蔗糖含量的 H^2 高于葡萄糖、果糖和总糖,柠檬酸含量的 H^2 高于苹果酸,表明糖酸性状的变异主要来自遗传效应,不易受环境因素的影响。【结论】在‘串枝红’×‘骆驼黄’杏F₁代中,蔗糖、葡萄糖、果糖、苹果酸含量是由多基因控制的数量性状,而柠檬酸含量可能是主效基因控制的质量性状。在杂交后代中易获得高葡萄糖和果糖含量、低柠檬酸含量的单株。

关键词:杏;F₁群体;糖;酸;遗传变异

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Analysis of genetic variation of sugar and acid contents in F₁ population of apricot derived from ‘Chuanzihong’×‘Luotuo huang’

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Abstract:【Objective】The objective of present study is to analyze the genetic variation of sugar and acid contents in apricot F₁ population in order to provide a basis for selecting parents in cross breeding of apricot.【Methods】Crossing was carried out between ‘Chuanzihong’ and ‘Luotuo huang’ in Beijing. The contents of sucrose, glucose and fructose of the fruits of two parents and their progenies were investigated with ion chromatography, and malic acid and citric acid were determined by high performance liquid chromatography (HPLC) method. About 1 kg fruits with the same maturity for each hybrid individual were randomly taken from the middle of the peripheral crown in four directions on 9:00—11:00, and then put into a 4 °C box and brought back to the laboratory. The fruits were kept at 4 °C in a fridge and evaluated within 1 day. The samples for each hybrid were divided into 3 portions as three replicates. The middle of pulp was homogenized and divided into 2 parts and stored in the refrigerator at -70 °C. One part was used to determine the contents of sugars, and the other to determine the contents of acids. Five trees of each parent were selected to determine the content of sugar and acid components, and the sampling method was the same as above. The contents of sugar and acid components

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were used to calculate the variance of the parents. The solutions of the apricot hybrids containing released sugars were detected by Dionex ICS-3000 Ion chromatograph. Sucrose, glucose and fructose were separated on CarboPac PA1 4 mm×250 mm (with a CarboPac PA1 4 mm×50 mm guard column) at 30 °C with injection volume of 10 μL using 200 mmol·L⁻¹ sodium eluting hydroxide as leaching liquid at the rate of 1 mL·min⁻¹ detected by pulsed amperometric detector (Au electrode). The organic acids of apricot hybrids were analyzed by Dionex P680 High-performance liquid chromatography. Malate and citrate were detected with a DIONEX PAD-100 detector. The Agilent poroshell 120 SB-C18 column (250 mm×4.6 mm i.d., 2.7 μm particle size) with a guard column cartridge (Sunchrom C18 cartridge) was used to maintain at 30 °C. Samples were eluted with 0.02 mol·L⁻¹ M solution (M indicated A:B=99.5:0.5, A indicated that 2.28 g K₂HPO₄·3H₂O dissolved in 1 L of water, adjusted with H₃PO₄ to pH=2.7; B indicates methanol) at the rate of 1 mL·min⁻¹ at pH=2.4 and detected by UV absorbance at 210 nm.【Results】The sucrose was the main sugar in soluble sugars of the fruits of apricot hybrids, whose variation range was 67.60–109.10 mg·g⁻¹ and 19.50–92.60 mg·g⁻¹ in 2015 and 2016, respectively. Sugar and acid components (except for the citric acid), total sugar and total acid showed a normal distribution, indicating that they were quantitative traits controlled by multiple genes, while citric acid presented a skewed distribution, implying that acid contents were qualitative traits and might be controlled by both major gene and polygenes. The extreme values of different sugars, acid components and total sugar and total acid indicated that there were some promising individuals in the progenies which could be potentially used as parent for breeding high sugar or high acid apricot varieties. The populations exhibited a wide phenotypic variation in fructose, glucose, total sugar, tartaric acid, and total acid contents where the coefficient of variation (*CV*) of sugar and acid contents were over 20%, and the range of acid contents was higher than that of sugar contents, indicating that there was a larger selecting potential for acid content. The content of sucrose, citric acid and total acid of the hybrids were lower than the medium value, representing a decline variation. The broad sense heritability (*H²*) of fructose, glucose, total sugar, citric acid and total acid contents were over 0.70, in which the *H²* of sucrose was higher than that of glucose, fructose and total sugar and citric acid was higher than that of malic acid, indicating that variations of these traits mainly resulted in inheritance.【Conclusion】Sucrose, glucose, fructose and malic acid were the quantitative traits controlled by the multiple genes, while citric acid might be qualitative traits and might be controlled by both major gene and polygenes in the F₁ population of ‘Chuanzhihong’ and ‘Luotuohuang’.

Key words: Apricot; F₁ population; Sugar; Acid; Genetic variation

杏(*Prunus armeniaca*)属于蔷薇科(Rosaceae)植物,原产于中国,栽培历史悠久,早在3 500多年前就被人类认识、利用,与桃、李、栗和枣并称为“五果”,被广泛种植^[1]。杏是遗传背景复杂、杂合度高的多年生木本植物,果实中的糖酸等品质性状在杂交过程中分离广泛,给杂交后代中糖、酸含量分布规律的预测带来一定困难。通过构建杏F₁代群体,研究杏果实中糖酸性状的遗传特点及倾向是指导杏杂交育种工作的前提,并且为科学选配亲本提供理论依据,同时为构建遗传连锁图谱及定位性状基因奠定基础。

随着人们生活水平的不断提高,果实质品日益

受到关注。果实中糖酸组分、含量及其比例均会影响品质^[2-4]。杂交育种是果树遗传性状改良的重要手段之一,目标性状的遗传变异越大,从杂交后代中选出优异单株的概率越高^[5]。陈美霞等^[6]对‘凯特’与‘新世纪’杏杂种后代的风味物质遗传进行了初步研究,发现各糖酸组分的基因效应差异较大,基因的加性效应主要表现在蔗糖、苹果酸遗传上;基因的加性效应与非加性效应共存于果糖、葡萄糖、柠檬酸遗传中,而在草莓糖含量遗传中,非加性效应表现明显^[7]。在桃^[8]、杏^[9]和梨^[10]上的研究发现,果实中可溶性固形物含量和可溶性糖含量表现出连续正态分布的规律,可能是受多基因控制的数量性状,在苹果上

甜度表现为数量性状,其中果糖、葡萄糖、蔗糖含量是由微效基因控制的数量性状,而酸含量表现为质量性状,受单一基因控制^[11-13],但李俊才等^[14]研究发现,梨果实糖、酸含量均表现为数量性状。对脐橙糖酸遗传的亲本偏向性分析发现,苹果酸、柠檬酸的积累倾向于父本^[15]。通过以上分析表明,不同树种杂交后代果实中可溶性固形物、糖和酸含量的遗传变异复杂,糖酸的遗传规律及倾向因树种或杂交组合的不同而呈现出不同的结果。

在果树上关于糖酸性状遗传规律的研究已有诸多报道,但遗传变异规律因树种或品种不同存在较大差异。目前,在杏上已有关于糖酸遗传研究的报道,但以‘串枝红’×‘骆驼黄’为亲本杂交后代糖酸遗传规律的研究还未见报道。因此,笔者以杏品种‘串枝红’为母本,‘骆驼黄’为父本进行杂交,通过测定亲本及其F₁代群体成熟果实中蔗糖、葡萄糖、果糖、苹果酸和柠檬酸含量,探讨果实糖酸性状在杏F₁群体中的遗传特点和倾向,旨在为杏高品质育种中亲本的科学选配提供理论依据。

1 材料和方法

1.1 试验材料

以杏品种‘串枝红’(简称为C)为母本,‘骆驼黄’(简称为L)为父本,在2007年春进行套袋杂交,获得的种子经层积处理萌发后移至温室培养。2008年春将杂交苗定植在北京市农林科学院林业果树研究所杏育种基地,杂交后代株行距1.0 m×2.0 m,树形为开心形,杂交后代立地条件及田间管理措施一致。以100株杂交后代为试材,2015年有59株杂交后代结果,2016年有92株杂交后代结果。

为尽量保证亲本及后代果实成熟度的一致性,取样由同一人完成。样品采集于上午09:00—11:00进行,每株树从东、南、西、北4个方向随机选取无病虫害的果实约1 kg,将混合后的样品分成3份,作为3个重复。将采好的果实装入冰壶带回实验室后去皮,取中部果肉进行匀浆处理,之后分为2份置于-70℃冰箱保存,其中一份用于糖组分含量的测定,另一份用于各酸组分含量的测定。每个亲本选取长势基本一致的5株,用于果实中糖酸组分含量的测定,取样方法同上,测定结果用于计算亲本的方差。

1.2 试验方法

杏果实中糖酸的提取、测定和高效液相色谱条

件参照姜凤超等^[16]的方法。

1.3 数据分析

数据均采用Excel 2013进行整理,运用SPSS 24.0软件进行统计分析与绘图。总糖含量为蔗糖、葡萄糖和果糖含量之和,总酸含量为苹果酸和柠檬酸含量之和。广义遗传力(H²)参照Chen等^[17]的方法:

$$\sigma_E^2 = (\sigma_f^2 + \sigma_m^2)/2;$$

$$H^2 = (\sigma_p^2 + \sigma_E^2)/\sigma_p^2.$$

其中,σ_f²和σ_m²分别代表母本和父本的表型方差,σ_p²和σ_E²分别代表遗传方差和环境方差。

变异系数(CV)参照崔艳波等^[18]的方法:

CV% = σ/F × 100。其中,F为后代平均值,σ为标准差。

2 结果与分析

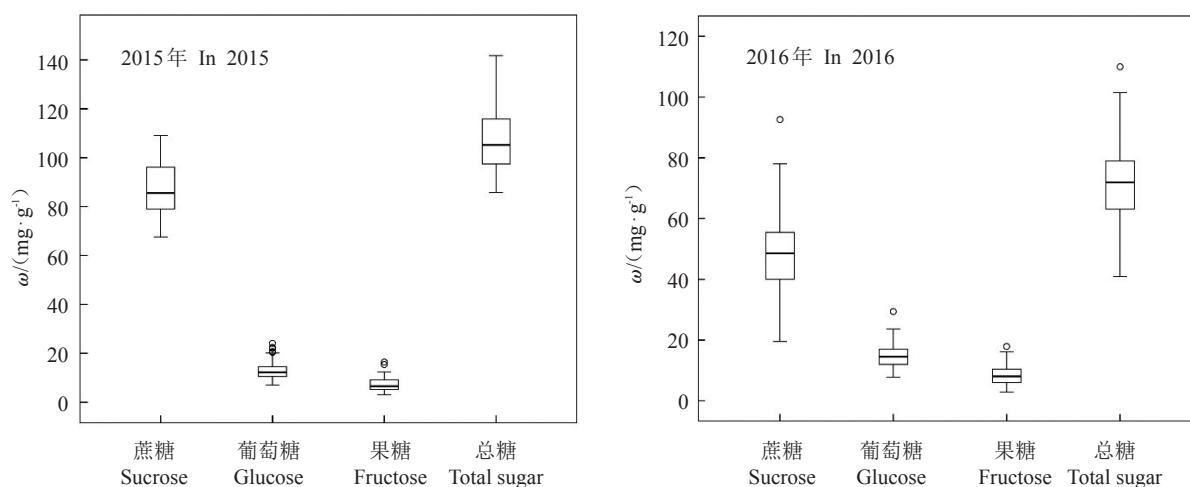
2.1 F₁代群体果实糖、酸含量及其分布范围

2.1.1 糖组分与总糖含量及其分布 如图1所示,‘串枝红’×‘骆驼黄’杂交后代果实以积累蔗糖为主,并且蔗糖含量(ω)的变化范围在2015、2016年分别为67.60~109.10、19.50~92.60 mg·g⁻¹,显著大于葡萄糖与果糖含量的变化范围。不同年份间杂交后代果实中糖组分与总糖含量的趋向性不同,2015年趋向低糖区域,而2016年则趋向中间区域,属于正态分布类型。2015年杂交群体果实中蔗糖和总糖含量高于2016年,而葡萄糖和果糖含量基本持平。不同糖组分及总糖含量均有极值存在,表明子代中有超亲单株出现,为选育高糖杏品种提供了材料。

2.1.2 酸组分与总含量及其分布 杏F₁代群体果实中柠檬酸、苹果酸和总酸含量的分布及变化范围如图2所示。杂交后代果实中苹果酸平均含量高于柠檬酸。杏杂交后代果实中苹果酸和总酸平均含量趋向于中间区域,而柠檬酸平均含量趋向于低酸区域,具有偏向低柠檬酸亲本的趋势,并且2a的数据均显示为同样的变化规律。不同年份间柠檬酸、苹果酸和总酸含量基本持平,柠檬酸和总酸含量有极值出现,表明杂交后代中有超亲单株出现,为选育高酸杏品种提供了材料。

2.2 F₁代群体果实糖、酸含量的频率分布

杏F₁代群体糖组分含量频次分布如图3所示,杂交后代的糖组分及总糖含量多集中在双亲之间,



箱体代表数据的集中分布范围,包含样本 50% 的数据,中间横线表示数据的中心位置,上下截止线之间包含了样本 99% 的数据。上下截止线外的°表示超出本体值外的极值。2015 年样品数为 59 个,2016 年样品数为 92 个。下同。

The box represents the central distribution of data. It indicates the distribution for 50% of the data. The middle line represents the center of the data, and the data between the upper and lower cut-off lines contains 99% of the sample data. The ° of upper and lower cut-off lines indicates the extreme value beyond the body value. The number of samples in 2015 and 2016 is 59 and 92, respectively. The same below.

图 1 杏 F₁ 群体果实糖组分含量及分布范围

Fig. 1 Content and distribution of sugar components in apricot F₁ population fruits

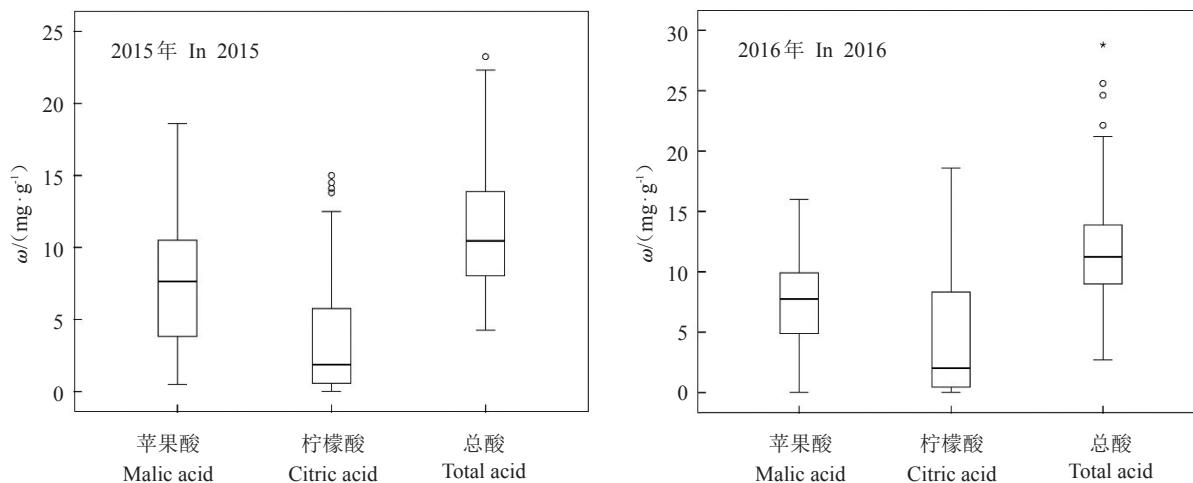


图 2 杏 F₁ 群体果实酸含量及分布范围

Fig. 2 Content and distribution of acid components in apricot F₁ population fruits

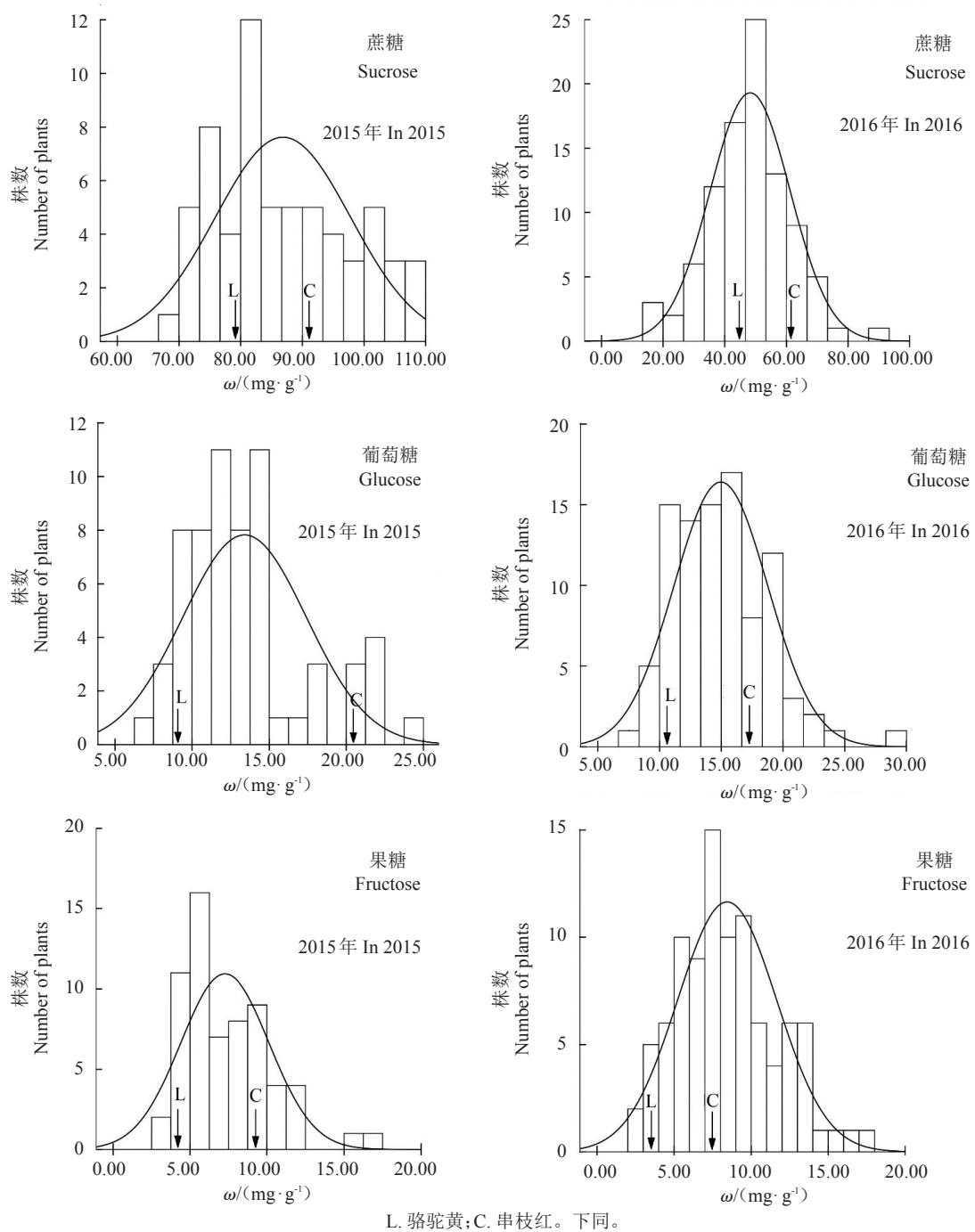
糖组分和总糖均为正态分布,并且不同年份的变化规律相似,说明杏果实的糖含量是多基因控制的数量性状。2016年糖组分及总糖含量在群体中的正态分布趋势优于2015年,这可能与2015年样本数量较少有关。

如图4所示,杂交后代的苹果酸含量绝大多数集中在双亲之间的区域,频率分布曲线呈正态分布,并且2 a的变化趋势基本一致,说明苹果酸含量属于多基因控制的数量性状;不同年份间柠檬酸含量多

集中在低酸区域,极高的后代所占比例较低,呈现偏正态分布,表明杏果实柠檬酸的遗传可能存在主效基因。杂交后代总糖与总酸含量多集中在双亲之间,总糖、总酸含量极低或极高的后代所占比例较低,呈正态分布(图5),说明杏果实中总糖和总酸是受多基因控制的数量性状。

2.3 F₁代群体果实糖、酸的遗传变异

不同年份间各糖酸组分(除蔗糖)及总酸含量在杂交后代中均出现广泛分离,变异系数均超过 20%



L. Luotuo Huang; C. Chuanzhihong. The same below.

图3 杏F₁群体糖组分含量频次分布Fig. 3 Frequency distribution of sugar contents in apricot F₁ population fruits

(表1),其中酸(苹果酸、柠檬酸和总酸)含量的变异系数均高于糖(蔗糖、葡萄糖、果糖和总糖)含量,表明酸的选择潜力更大。不同年份间,杂交后代葡萄糖、果糖和苹果酸含量的平均值高于亲中值,表明这三个组分的遗传主要不仅存在加性效应,还存在一定的非加性效应,而蔗糖、柠檬酸和总酸含量低于亲中值,表现为衰退变异,主要受基因的加性效应影

响。糖酸性状的广义遗传力(H^2)较高,均在0.70以上,酸组分含量的 H^2 高于糖组分,其中蔗糖含量的 H^2 高于葡萄糖、果糖和总糖,柠檬酸含量的 H^2 高于苹果酸和总酸,糖酸比的 H^2 在0.90以上,以上表明糖酸性状的变异主要来自遗传效应,并且酸的遗传效应大于糖,更不易受环境因素影响,糖酸比的变异主要受亲本遗传效应的影响。

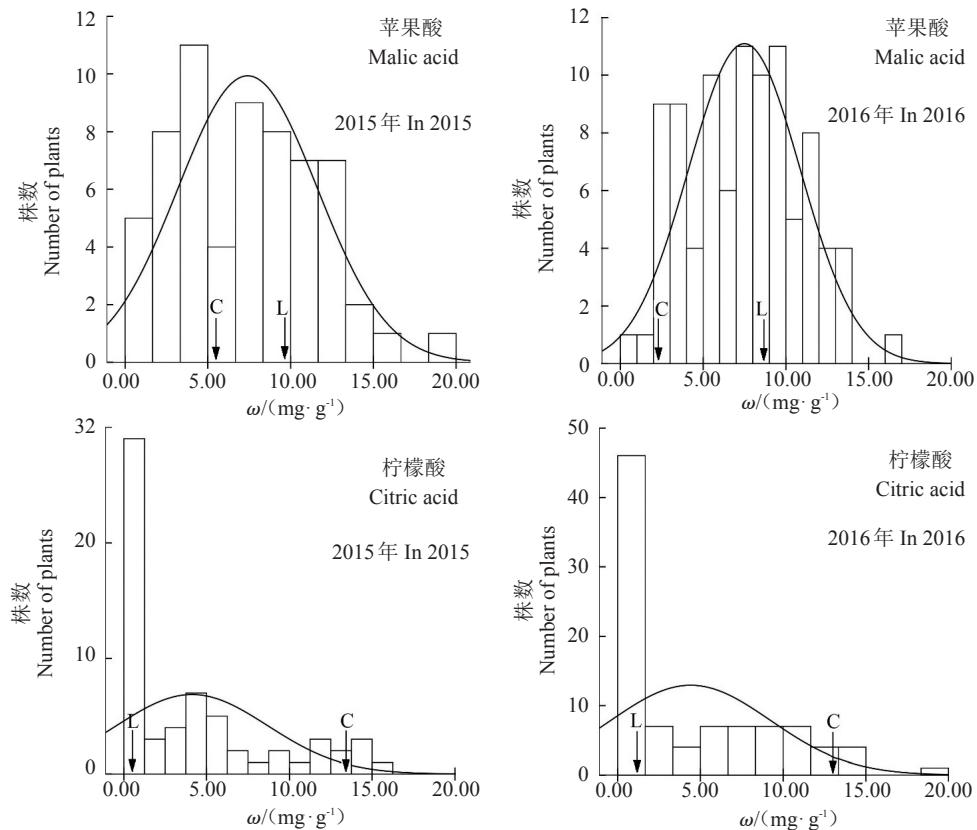
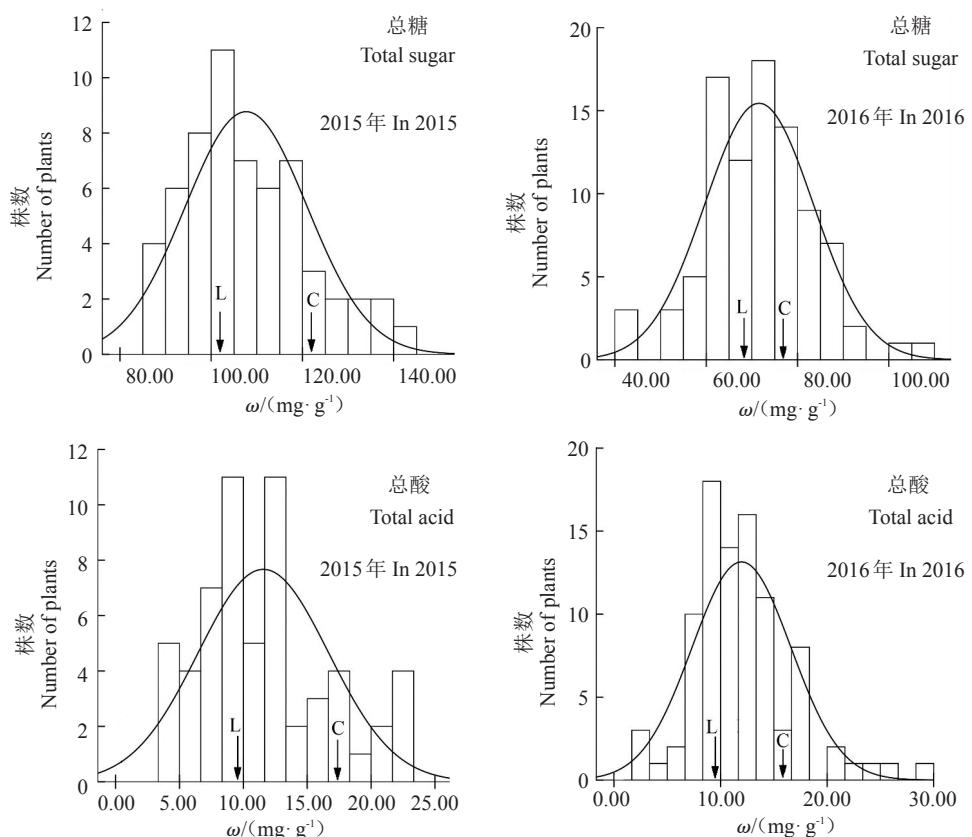
图4 杏F₁群体酸组分含量频次分布Fig. 4 Frequency distribution of acid contents in apricot F₁ population fruits图5 杏F₁群体总糖、总酸含量频次分布Fig. 5 Frequency distribution of total acids and sugars in apricot F₁ population fruits

表1 杏F₁群体果实糖、酸组分的遗传变异Table 1 The hereditary variation of sugar and acid components in apricot F₁ population fruits

年份 Year	性状 Trait	亲本 Parents		亲本平均值 Cross parents value	F ₁ 群体 F ₁ population 后代平均值±标准差 Progeny average value± standard deviation	变异系数 Coefficient of variation, CV%	广义遗传力 Broad sense heritability, H ^f
		串枝红 Chuanzihong	骆驼黄 Luotuo huang				
2015	ω(蔗糖) Sucrose content/(mg·g ⁻¹)	92.10±5.17	80.30±5.60	86.20	84.21±7.84	12.77	0.88
	ω(葡萄糖) Glucose content/(mg·g ⁻¹)	21.50±1.17	8.51±0.57	15.01	16.33±1.13	29.70	0.87
	ω(果糖) Fructose content/(mg·g ⁻¹)	8.89±0.56	4.24±0.23	6.57	7.24±0.44	39.72	0.78
	ω(苹果酸) Malic acid content/(mg·g ⁻¹)	3.83±0.22	9.43±0.88	6.63	7.48±0.60	56.68	0.75
	ω(柠檬酸) Citric acid content/(mg·g ⁻¹)	13.40±1.33	0.46±0.03	6.93	4.08±0.68	110.65	0.85
	ω(总糖) Total sugar content/(mg·g ⁻¹)	122.49±10.98	93.05±6.09	107.77	107.66±7.74	12.46	0.81
	ω(总酸) Total acid content/(mg·g ⁻¹)	17.23±1.37	9.80±0.53	13.56	11.57±0.78	44.21	0.83
	糖酸比 Sugar-acid ratio	7.11±0.69	9.41±0.91	8.26	9.31±0.52	63.42	0.98
2016	ω(蔗糖) Sucrose content/(mg·g ⁻¹)	59.20±4.91	48.60±2.66	53.90	48.12±2.71	27.11	0.85
	ω(葡萄糖) Glucose content/(mg·g ⁻¹)	16.70±1.10	11.10±0.81	13.90	14.99±1.04	25.52	0.84
	ω(果糖) Fructose content/(mg·g ⁻¹)	6.76±0.45	3.95±0.25	7.33	8.46±0.52	38.39	0.82
	ω(苹果酸) Malic acid content/(mg·g ⁻¹)	2.14±0.18	8.99±0.59	5.57	7.53±0.32	44.71	0.82
	ω(柠檬酸) Citric acid content/(mg·g ⁻¹)	12.25±0.62	0.71±0.06	6.48	4.43±0.47	109.84	0.88
	ω(总糖) Total sugar content/(mg·g ⁻¹)	82.66±6.54	67.59±3.68	75.13	71.57±6.16	21.30	0.71
	ω(总酸) Total acid content/(mg·g ⁻¹)	14.39±1.22	9.70±0.90	12.05	11.96±1.19	38.90	0.77
	糖酸比 Sugar-acid ratio	5.74±0.30	6.97±0.63	6.36	5.98±0.43	67.64	0.93

3 讨 论

不同树种间果实中糖酸组分含量并不相同。在桃果实中蔗糖含量>葡萄糖、果糖含量>山梨醇含量,主要有机酸为苹果酸^[3,18-19];樱桃果实以葡萄糖含量最高,果糖含量最低,有机酸以苹果酸含量最高,柠檬酸次之^[20]。本研究结果表明,杏果实中糖组分以蔗糖为主,酸组分以苹果酸或柠檬酸为主,这与前人报道的结果一致^[21-23]。本研究中不同年份间糖酸组分含量差异较大,可能与2016年果实成熟前降水多于2015年有关。研究表明,增加水分供应会导致果实中各糖酸组分含量的下降^[24]。

在梨上的研究发现,苹果酸和柠檬酸在杂种后代中均表现出典型的数量性状遗传特征^[25-26],但闫忠业等^[13]在苹果上的研究发现柠檬酸符合质量性状,受主效基因控制。本研究中,F₁群体中杏果实苹果酸和总酸含量呈正态分布,而柠檬酸含量呈偏正态分布,说明苹果酸和总酸为多基因控制的数量性状,而柠檬酸可能是受主效基因控制的质量性状。陈美霞等^[6]发现柠檬酸遗传不仅存在加性效应,还存在一定的非加性效应,而本研究结果表明,柠檬酸遗传主要受加性效应影响,该差异可能与选择的亲本不同有关。在本研究中,杏杂交群体中酸组分广义遗传力(H^f)均在0.75以上,说明酸性状在后代中可以稳定遗传,不易受环境影响。亲本有机酸积累类型

并不相同,母本‘串枝红’属于柠檬酸积累型,父本‘骆驼黄’属于苹果酸积累型,在F₁群体中杏果实苹果酸含量的平均值高于亲中值,而柠檬酸和总酸含量低于亲中值,表明杂交后代中苹果酸含量的遗传倾向于高苹果酸含量的亲本,而柠檬酸和总酸含量的遗传倾向于低柠檬酸和总酸含量的亲本,这为有机酸育种亲本选配提供了理论依据。

笔者发现,杏F₁群体中糖组分和总糖含量均呈正态分布,在杂交后代中呈连续变异,具有典型的数量性状遗传特征,这与前人在其他果树上报道的结果一致^[13,25]。在本研究中,杏杂交群体中糖组分的广义遗传力(H^f)均在0.70以上,说明糖性状的变异受环境影响较小,主要来自遗传效应。蔗糖是杏果实中主要的可溶性糖,其遗传主要表现为加性效应,这与陈美霞等^[6]的结果一致。不同年份间杂交后代葡萄糖、果糖含量的平均值高于亲中值,而蔗糖含量低于亲中值,表明杂交后代中糖的遗传主要倾向于高葡萄糖、高果糖、低蔗糖含量亲本,而糖含量遗传倾向的研究对于指导亲本的科学选配具有重要意义。

细胞核遗传是杂交育种过程中主要的遗传形式,但在杂交后代中也存在一些性状变异倾向于母本,表现为母性遗传,为了进一步确认杏糖酸遗传规律,应该在将来的育种工作中进行反交试验验证。

4 结 论

‘串枝红’×‘骆驼黄’杏F₁群体果实中可溶性糖以蔗糖为主;蔗糖、葡萄糖、果糖和苹果酸含量在杂交后代中为数量性状,而柠檬酸含量可能是受主效基因控制的质量性状;葡萄糖、果糖和苹果酸含量的遗传不仅存在加性效应,还存在一定的非加性效应,而蔗糖、柠檬酸和总酸含量主要受基因的加性效应影响;根据可溶性糖和有机酸含量的遗传倾向可知,在杂交后代中易获得高葡萄糖和果糖含量、低柠檬酸含量的单株。

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