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菠萝蜜果实中糖分积累特征及相关代谢酶活性分析

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摘 要:【**目的**】探究菠萝蜜果实中的糖分组成及含量积累特征。【**方法**】以菠萝蜜品种'马来西亚1号'为材料,利用高效液相色谱法分析不同发育时期果肉中蔗糖、果糖和葡萄糖含量,应用分光光度计法检测淀粉含量及相关代谢酶活性。【**结果**】菠萝蜜成熟果实中蔗糖含量最高,超过总糖含量的70%,主要在果实采后成熟期积累。果糖和葡萄糖含量接近,各占总糖的15%左右。淀粉是菠萝蜜果实中重要的非结构性碳水化合物,在果实成熟采摘前积累、后熟期间降解。蔗糖酸性转化酶(AI)为主要的蔗糖水解酶,与蔗糖含量呈显著负相关(相关系数为-0.602*)。蔗糖合成酶(SUSY)、蔗糖磷酸合成酶(SPS)在后熟阶段活性最高,与蔗糖含量呈显著正相关(相关系数分别为0.915**、0.997**),参与蔗糖的合成。腺苷二磷酸葡萄糖焦磷酸化酶(AGPase)在果实发育中期活性最高,与淀粉含量呈显著正相关(相关系数为0.900*)。α-淀粉酶在后熟阶段活力最高。【**结论**】蔗糖是'马来西亚1号'菠萝蜜果肉的主要糖分,蔗糖的积累与AI活性呈显著负相关,与SUSY、SPS活性呈显著正相关,主要在后熟期积累。淀粉是菠萝蜜果实发育的主要非结构性碳水化合物。淀粉的积累与AGPase活性呈显著正相关,在果实成熟前合成、后熟期间降解。

关键词:菠萝蜜;果实发育;糖分积累;酶活性

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Characterization of sugar accumulation and enzyme activities in jackfruit

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Abstract:【Objective】Sugars are a key component in fruits, and their composition and contents affect the flavor of fruits. Sugars not only provide energy for plant development, but also contribute to the quality of sink tissues. *Artocarpus heterophyllus* Lam., commonly known as jackfruit, produces the largest tree-borne fruit known thus far. The fruit contains many sugar-derived compounds including carotenoids, flavonoids, sterols and terpenes, which contribute the unique flavor to jackfruit. The degradation and synthesis system of sucrose determines the sugar composition in the fruit. In order to characterize sugar composition and accumulation in jackfruit, the concentrations of sucrose, glucose, fructose and starch were determined. Meanwhile, the activities of sucrose and starch metabolism-related enzymes were analyzed in order to provide the important information on sugar metabolism and provide a useful reference for further research of fruit development in jackfruit.【Methods】Fruit of 'Malaysia-1' cultivated in an experimental field at Xinglong tropical garden (Wanning, Hainan, China) were collected from three trees at different developmental stages for the experiment. Fruit were tagged on the day of pollination. Perianth tissues were removed carefully from the fruit samples at different developmental stages (at 50, 70, 90, 110, 117, and 120 days after pollination). Frozen powdered tissue (3 g) was homogenized in 10 mL of 80% alcohol with ribitol as an internal standard, and centrifuged at 10 000 r for 15 min at 4 ℃. The supernatant was transferred into a new tube, vacuum dried under ambient temperature and then re-dissolved. The solution was filtered through a 0.45

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μm membrane filter prior to analysis. The contents of sucrose, glucose and fructose in jackfruit were measured by high performance liquid chromatography (HPLC). For enzyme activity assay, 0.1 g of powdered sample was homogenized in 5 mL of Mops-NaOH buffer (50 mmol·L^{-1}, pH 7.2) containing 5 mmol·L^{-1} $MgCl_2$, 1 mmol·L^{-1} EDTA, 20 mmol·L^{-1} β-mercaptoethanol, 5% PVPP, and 1% BSA. After incubation in ice for 30 min, the homogenates were centrifuged at 10 000 *g* for 15 min. The supernatant was used to determine enzyme activity. The content of starch and the activities of related enzymes were measured using spectrophotography. Sugar metabolism was characterized by evaluating correlations between enzyme activity and sugar accumulation during fruit development. 【Results】The sucrose concentration was less than 1 g·kg^{-1} before 90 DAP, but it increased significantly to 165 g·kg^{-1} at 120 DAP. In mature fruit, sucrose concentration was the dominant sugar accounting for approximately 70% of total sugars. Glucose and fructose contents were similar, and they were approximately 13 g·kg^{-1} from 50 DAP to 90 DAP, before a two-fold decrease at 110 DAP, and then increased to about 20 g·kg^{-1} at 117 and 120 DAP. Each of them accounted for approximately 10% of the total sugars. Starch was an important non-structural carbohydrate in jackfruit. Starch concentration increased from 50 DAP (12.8 g·kg^{-1}) to a highest level at 110 DAP (148 g·kg^{-1}), and then decreased as the fruit matured. The enzyme AI (acid invertase) was active from 50 to 90 DAP and its activity decreased from 110 to 120 DAP. Its activity was significantly negatively correlated to sucrose concentration (r=-0.602^{*}). The activities of sucrose synthase (SUSY) and sucrose phosphate synthase (SPS) were high at 117 and 120 DAP. Their activities were positively correlated with sucrose content (r=0.915^{**}, 0.997^{**}, respectively). Adenosine diphosphoglucose pyrophosphprylase (AGPase), an important enzyme in starch metabolism, had the highest activity at mature stage, and had a positive correlation with starch content during fruit development (R=0.900^{**}). The activity of α-amylase was high at repining stage. 【Conclusion】Sucrose is the main sugar in jackfruit, which has a negative correlation with AI activity and positive correlations with SUSY and SPS activities. Starch has a positive correlation with AGPase. We suggest that developmental changes in sugar and starch concentrations appear to result from the coordinated actions of three factors. First, during the early fruit development, AI and SUSY are involved in sucrose hydrolysis and unloading. However, as the primary demand for sucrose at this stage is for growth, there is little excess glycogen for sugar accumulation, resulting in low concentrations of sucrose, glucose, fructose and starch. Second, as the fruit matures, starch accumulation reaches a peak level. Third, during fruit ripening (after 110 DAP), starch breaks down and sucrose begins to accumulate, leading to increase in the concentration of total soluble sugars and thus the sweetness of the fruit. From an evolutionary perspective, the sweetness of the mature fruits attracts animals for seed dispersal. These results suggest that sugar mechanism is intimately associated with fruit development.

Key words: Jackfruit; Fruit development; Sugar accumulation; Enzyme activity

糖分是果实的重要构成,果实内的糖类物质以及它们的中间代谢产物是果实次生代谢的底物,广泛影响果实的风味物质、呈色物质、特征香气物质的形成[1]。糖分的合成起始于叶片光合作用产生的蔗糖。蔗糖经韧皮部运输至库细胞,再通过质外体运输或共质体运输进入库细胞。在库细胞中,蔗糖在相关转化酶和蔗糖合成酶的作用下分解成葡萄糖、果糖,也可以再次合成新的蔗糖[2-3]。因此,蔗糖、葡萄糖、果糖是水果中主要的糖分,糖类物质种类和含量的差异构成了风味各异的水果品种。运输到库细胞的蔗糖还可以在蔗糖合成酶的作用下水解成尿苷二磷酸葡萄糖(UDP-glucose)和果糖。尿苷二磷酸葡萄糖和葡萄糖在磷酸酶的作用下生成6-磷酸葡萄糖,为淀粉的合成提供前体[4-5]。果实中糖分除了

作为甜味和能量物质储存外，它们还是下游次生代谢的前体物质。葡萄糖通过糖酵解途径分解成丙酮酸并释放生理活动所需能量[6]。糖酵解途径的中间产物3-磷酸甘油醛、丙酮酸通过甲基赤藓糖-4-磷酸(MEP)途径或甲羟戊酸(MVA)途径生成牻牛儿基二磷酸，为植物萜类物质的合成提供前体[7]。另外，糖酵解途径中D-磷酸赤藓糖和磷酸烯醇丙酮酸是莽草酸途径的直接前体。莽草酸途径是植物苯丙素类物质合成的上游反应，在植物芳香物质、生物碱合成代谢中发挥重要作用[8-9]。综上所述，果实糖代谢特征系统地影响了果实的甜度、香气、营养成分等品质指标。

菠萝蜜(*Artocarpus heterophyllus* Lam.)在植物分类学中又名波罗蜜、木菠萝、牛肚子果，是典型的热带水果，其果肉为宿存的花被，味道清甜、香气独特、营养丰富，有热带水果皇后、齿留香等美称，在我国热带及南亚热带地区广泛种植[10]。随着旅游业的发展及人民生活水平的提高，市场对菠萝蜜的需求量越来越大，菠萝蜜拥有广阔的市场前景。笔者以海南省菠萝蜜主栽品种‘马来西亚1号’为试验材料，检测果实发育过程中主要糖分含量及代谢相关酶活性，旨在探索菠萝果实糖积累特征，为后续研究下游次生代谢及主要品质性状的形成奠定基础。

1 材料和方法

1.1 材料

试验材料为海南省主栽品种‘马来西亚1号’，果肉(宿存的花被)取自中国热带农业科学院香料饮料研究所菠萝蜜种质资源圃。根据菠萝蜜果实发育特征，将果实发育分为4个典型时期：果肉形成期(开花后30~50 d)、快速膨大期(开花后50~90 d)、成熟采摘期(90~110 d)、后熟期(开花后110~120 d)。从雌花柱头长出为起始，取开花后50、70、90、110(成熟采摘期)、117(采摘后熟)、120 d(树上自然成熟)的果肉，每次随机取3个不同果实的果肉，-80 ℃保存。试验设3个重复，每个重复测定3次，取平均值。

1.2 蔗糖、果糖、葡萄糖、淀粉的提取与测定

菠萝蜜果肉中糖的提取参考李映志等[10]的高效液相色谱法进行。将上述果肉加液氮成分研磨，称取1.00 g果肉，加入5 mL 80%(φ)的乙醇于37 ℃水浴提取10 min，10 000 r·min^{-1}，离心5 min，吸出上清液，重复提取3次，合并上清液，90 ℃水浴蒸干浓缩，用超纯水溶解定容至10 mL，经0.45 μm滤膜过滤后上机分析。糖分检测采用高效液相色谱法，分析柱为CHO-820钙型糖柱，柱温90 ℃，流动相为超纯水，流速0.3 mL·min^{-1}，进样体积10 μL，用示差折光检测器检测，外标法定性定量。

淀粉的提取、检测参照sigma淀粉检测试剂盒(STA20-1KT)的方法进行。

1.3 酶的提取与检测

取上述0.1 g果肉粉末，加入5 mL的Mops-NaOH[11](50 mmol·L^{-1}，pH 7.2，含5 mmol·L^{-1} $MgCl_2$，1 mmol·L^{-1} EDTA，20 mmol·L^{-1} mercaptoethanol，5% PVPP，1% BSA)。冰上孵育提取30 min，10 000 r·min^{-1}，离心10 min，收集上清液作为酶提取液，用于后续活性检测。

在不同的pH条件下，蔗糖被酸性转化酶(AI)和中性转化酶(NI)分解为还原糖，还原糖与3,5－二硝基水杨酸反应生成棕红色氨基化合物，在510 nm有特征光吸收。因此，在一定范围内510 nm光吸收增加速率与转化酶的活性成正比。根据该原理检测AI和NI的活性，具体步骤参照Batta等[12]的方法。

蔗糖合成酶(SUSY)催化游离果糖与葡萄糖供体UDPG反应生成蔗糖，蔗糖磷酸合成酶(SPS)催化果糖-6-磷酸形成蔗糖磷酸，蔗糖和蔗糖磷酸可以与间苯二酚反应可呈现颜色变化，在480 nm下有特征吸收峰，酶活力大小与颜色的深浅成正比。根据该原理检测蔗糖合成酶和蔗糖磷酸合成酶的活性，具体步骤参照Hubbard等[13]的方法。

腺苷二磷酸葡萄糖焦磷酸化酶(AGPase)催化的逆向反应生成G1P，在反应体系中添加的磷酸己糖变位酶和6-磷酸葡萄糖脱氢酶依次催化生成6-磷酸葡萄糖酸和NADPH，在340 nm下测定NADPH增加速率，即可计算AGPase的活性。具体步骤参照Rodríguez-López等[14]的方法。

α-淀粉酶可随机地作用于淀粉中的α-1,4-糖苷键，生成葡萄糖、麦芽糖、麦芽三糖、糊精等还原糖。还原糖与3,5－二硝基水杨酸反应生成棕红色氨基化合物，在510 nm有特征光吸收。通过510 nm光吸收增加速率检测α-淀粉酶活性。

每g组织每min催化产生1 μmol·L^{-1}的蔗糖或葡萄糖定义为1个酶活单位(U)。酶活性的计算公式为：U(μmol·min^{-1}·g^{-1}，以鲜质量计)=(C×*Vt*×

1 000)/(FW×t×Vs×W),式中C为从标准曲线计算出检测的蔗糖的葡萄糖量/mg;Vt为提取酶液总体积/mL;FW为样品鲜质量/g;t为反应时间/min;Vs为测定时取用酶液体积/mL;W为检测物质的摩尔质量分数。

1.4　数据分析

试验数据采用Excel、SPSS软件进行分析。

2　结果与分析

2.1　菠萝蜜果肉糖组分及积累特征分析

通过高效液相色谱法测定开花后50、70、90、110(成熟采摘期)、117(采摘后7 d)、120 d菠萝蜜果肉中蔗糖、果糖、葡萄糖含量。从图1可以看出,葡萄糖、果糖在果肉中的含量及变化趋势比较一致。在开花后50、70、90 d的果肉中(果实成熟之前),葡萄糖质量分数分别为14.8、14.1、12.4 g·kg^{-1},果糖质量分数为14.5、14.4、13.3 g·kg^{-1}。成熟阶段(开花后110 d)葡萄糖、果糖质量分数明显降低,分别为6.7和7.5 g·kg^{-1}。在后熟阶段(开花后117、120 d)葡萄糖质量分数上升为22.1和21.9 g·kg^{-1},果糖质量分数上升为21.6和22.9 g·kg^{-1}。蔗糖在未成熟的果肉中质量分数均不足1.0 g·kg^{-1}(开花后50、70、90 d),在成熟的果实中上升为32.2 g·kg^{-1}(开花后110 d),在开花后117、120 d的后熟阶段大量积累,质量分数分别为142.3 g·kg^{-1}和165.7 g·kg^{-1}。由此可见,蔗糖是菠萝蜜成熟果肉中主要的糖分组成,决定了果肉的甜度。

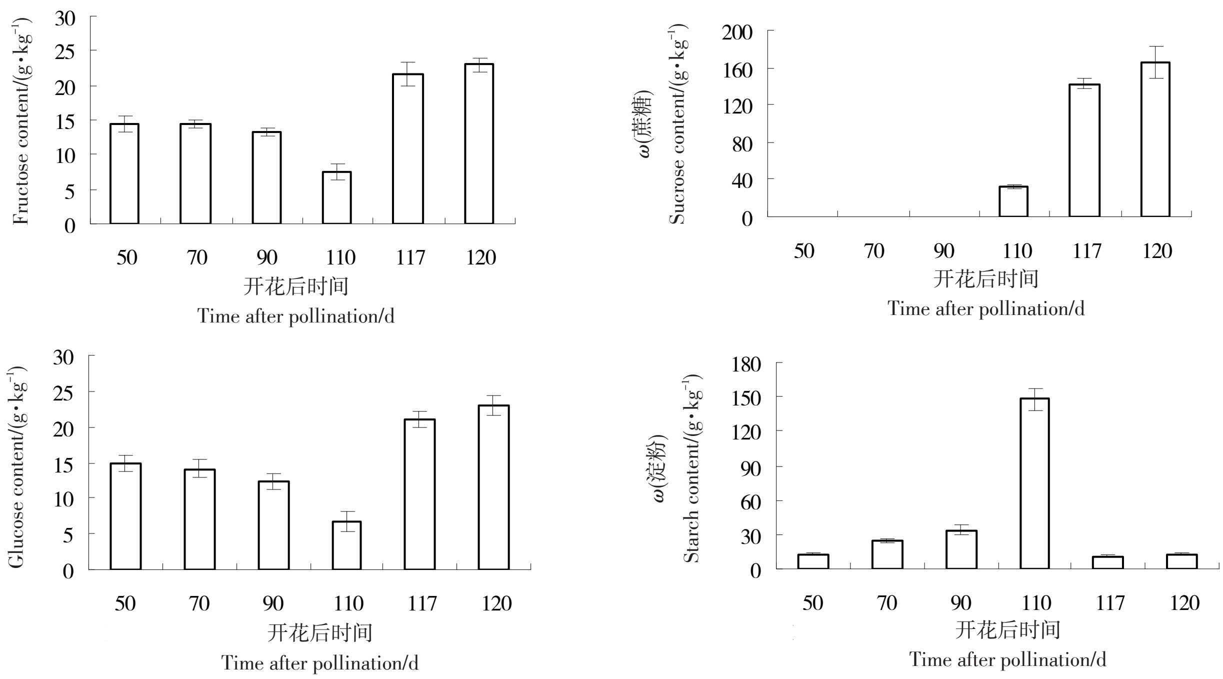

图1　果糖、蔗糖、葡萄糖、淀粉在不同发育时期果肉中的含量

Fig. 1 Concentrations of fructose, glucose, sucrose and starch in jackfruit at different developmental stages

淀粉是库组织中重要的能量储存形式,在菠萝蜜开花后50、70、90 d(成熟之前)的果肉中质量分数分别为12.8、23.7、33.8 g·kg^{-1},在开花后110 d果肉中,淀粉质量分数急剧上升为148 g·kg^{-1},而在后熟阶段又迅速降低为10.9 g·kg^{-1}(开花后117 d)和12.7 g·kg^{-1}(开花后120 d)。

2.2　糖代谢相关关键酶活性分析

2.2.1　*蔗糖代谢相关酶活性分析*　根据主要糖分的检测结果,首先分析蔗糖代谢相关的AI、NI、SPS和SUSY活性。如图2所示,AI在果实成熟前活力较高,保持在7.2~13.6 U,在成熟期及后熟期活力降低(2.4~3.9 U)。NI的活性则呈现与AI相反的趋势,随着果实的发育逐渐升高,在成熟期果实中迅速上升,在后熟期达到最高。但整体酶活性低于AI,最高仅为0.9 U。SUSY在果实发育初期活力较低(0.8~1.2 U),随着果实的发育,活力从成熟期开始增强,在后熟期达到最高(18.4 U)。SPS的活力呈现了类似的趋势,在成熟期前活力较低(0.8~1.2 U),在后熟期活力增强,并达到最高(14.6~18.4 U)。

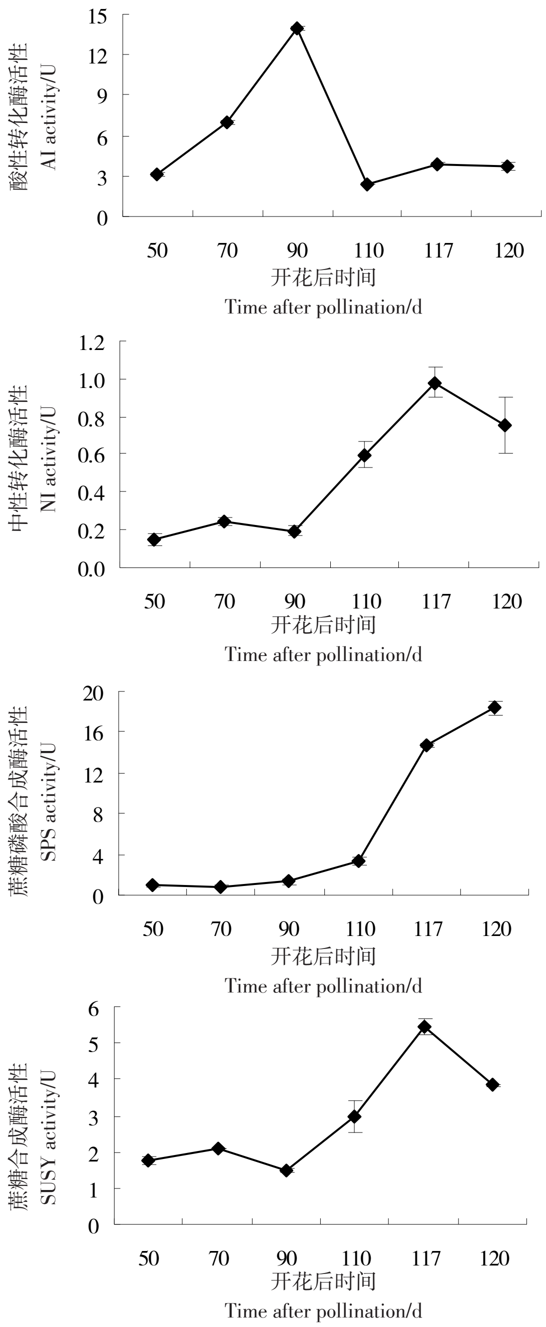

图 2 菠萝蜜果实发育过程中主要的蔗糖代谢相关酶活性变化

Fig. 2 Changes in activities of key enzymes involved in sucrose metabolism during fruit development

2.2.2 淀粉代谢相关酶活性分析 AGPase是淀粉合成的限速酶，检测结果如图3所示，该酶的活力随着果实的发育逐渐升高，在开花后110 d果肉中达到最高(41.2 U)，而后熟阶段活力急剧降低至10 U以下。α-淀粉酶是重要的淀粉降解酶。该酶在果实发育初期活力较低(1.8~4.5 U)，随着果实的发育，活力从成熟期开始增强(16.5 U)，在后熟期达到最高(60 U)(图3)。

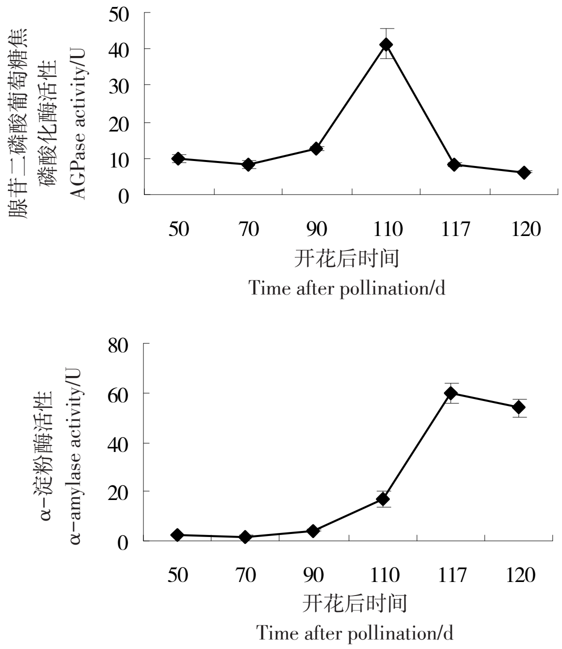

图 3 菠萝蜜果实发育过程中主要的淀粉代谢相关酶活性变化

Fig. 3 Changes in the activities of key enzymes involved in starch metabolism during fruit development

2.3 蔗糖、淀粉含量与代谢酶活性的相关性

对果实发育过程中蔗糖、淀粉含量与主要的代谢酶活性进行相关性分析(表1)，结果表明，蔗糖含量与AI活性呈显著负相关(相关系数为-0.602*)，与SUSY、SPS和NI活性呈显著正相关(相关系数分别为0.915**、0.997**、0.997**)。淀粉含量与AGPase活

表 1 蔗糖、淀粉含量与代谢酶活性的相关性

Table 1 Correlations coefficients between sugar contents and enzyme activities

	酸性转化酶活性 AI activity	中性转化酶活性 NI activity	蔗糖合成酶活性 SUSY activity	蔗糖磷酸合成酶活性 SPS activity	腺苷二磷酸葡萄糖焦磷酸化酶活性 AGPase activity	α-淀粉酶活性 α-amylase activity
蔗糖含量 Sucrose concentration	-0.702*	0.997**	0.915**	0.997**	-	-
淀粉含量 Starch concentration	-	-	-	-	0.900**	-0.223

注：**和*分别代表在 0.01 和 0.05 水平上显著相关。

Note: ** and * mean significant at 0.01 and 0.05 level, respectively.

性呈显著正相关(相关系数为0.900**),而与α-淀粉酶活性相关不显著(相关系数为-0.223)。

3 讨 论

糖分的组成是果实风味品质的重要指标,其组分和含量的差异影响了不同水果的风味,如樱桃主要含有葡萄糖和果糖,苹果、梨等含有葡萄糖、果糖和蔗糖3种糖,白肉枇杷果肉中以蔗糖为主,而红肉枇杷中蔗糖、果糖、葡萄糖含量接近[15-18]。本研究中,菠萝蜜成熟果肉中蔗糖含量最高,超过总糖量的70%,主要在后熟阶段合成。果糖和葡萄糖含量及积累趋势比较相似,各占总糖量的15%左右,且不同发育阶段含量差异不大,由此可见蔗糖是菠萝蜜果实中主要的糖分。糖分的差异与糖代谢相关酶活性的差异息息相关,在菠萝蜜果实发育阶段,AI活性变化呈先升高后降低的趋势,与蔗糖的积累呈显著负相关。该结果与在龙眼、荔枝、柑橘等上的研究报道一致,即AI活性下降是蔗糖积累的必要前提[19-21]。另外,NI活性随着果实的发育活性增加,与蔗糖的含量变化呈显著正相关,可能与糖分进入液泡合成相关。蔗糖的含量与SUSY和SPS活性呈显著正相关,蔗糖积累的同时伴随着AI活性的下降和SS、SPS活性的提高,这与猕猴桃、杧果等水果类似,糖分积累进程是在蔗糖代谢相关酶的协同作用下进行的,菠萝蜜后熟期是甜味物质形成的关键时期[22-23]。

作为库细胞中重要的储藏性多糖之一,淀粉既是人类利用的能量和碳源,同时也是植物生长发育重要的能量来源[24]。菠萝蜜果实在成熟期积累了大量的淀粉,而在未成熟及后熟阶段含量较低。AGPase是淀粉合成的限速酶,该酶的活性与淀粉含量呈显著正相关,在菠萝蜜开花后90~110 d果实中活性最高,表明淀粉在成熟期大量合成。淀粉降解酶主要在菠萝蜜果肉后熟阶段活性较高,表明成熟期合成的淀粉在后熟阶段被降解。在香蕉、杧果等果实的后熟阶段,淀粉的水解和消失,是果实软化的重要原因[25-26]。菠萝蜜果实蔗糖的积累趋势表明,采摘后7 d和树上自然成熟的果实差别不大,说明在后熟阶段蔗糖的合成来自于果肉本身能量物质的转化,而不是依靠光合作用补给,由此我们推测,淀粉的降解除了与果实软化相关外,同时也是菠萝蜜后熟阶段果实发育的能量来源之一。该结果为研究果实后熟期品质指标的调控提供了思路。

4 结 论

蔗糖是菠萝蜜果实中主要的糖分,在果实发育初期进入库细胞的蔗糖由AI水解,为果肉的快速生长提供能量和碳源,因此没有蔗糖和淀粉等能量物质的积累。随着果实的发育,在开花后110 d左右,果实结束快速生长,装载进库细胞的能量物质最先合成淀粉,淀粉合成相关酶活性以及淀粉含量在成熟期最高。在果实的后熟阶段,淀粉降解,蔗糖在该阶段大量积累。

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