

扁桃内果皮木质化过程中相关酶活性的变化

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摘要:【目的】探讨扁桃内果皮的发育与木质素积累及相关酶活性的关系。【方法】以薄壳‘纸皮’和厚壳‘长石头’两个不同壳厚类型扁桃品种为试材, 分析内果皮不同发育时期木质素、纤维素和酚类物质含量及其相关酶活性的变化规律。【结果】两个扁桃木质化过程中木质素和纤维素含量均在积累, 酚类物质含量呈现下降趋势, PAL、CAD、C4H、PPO、POD活性呈现先上升后下降趋势; ‘长石头’扁桃内果皮木质素和纤维素含量分别在花后55 d和40 d起始终高于‘纸皮’, 但内果皮的酚类物质含量始终低于‘纸皮’, ‘长石头’扁桃内果皮PAL、CAD、C4H、PPO、POD活性高峰值显著高于‘纸皮’; 扁桃内果皮木质素与纤维素含量呈正相关, 而与酚类物质含量呈现负相关; PAL、CAD、C4H、PPO、POD活性与木质素快速积累后期呈现负相关。【结论】较高的PAL、CAD、C4H、PPO、POD活性和大量的木质素所需要的前物质促进了木质素的积累, 从而使内果皮木质化加厚。

关键词:扁桃; 内果皮; 木质化; 酶活性

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Changes in relative enzyme activities during the lignification in the almond endocarp

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Abstract:【Objective】Analysis of the relationship between lignin content in almond endocarp and related enzyme activity in the process of development reveals endocarp lignification and its mechanism. 【Methods】This study used thin shelled ‘Zhipi’ and thick shelled ‘Changshitou’ as the experimental materials. Lignin content, cellulose content, polyphenol content and related enzyme activities in almond endocarp were determined in different development periods and the correlations between various parameters were analyzed. 【Results】The endocarp development in the thin shelled ‘Zhipi’ and thick shelled ‘Changshitou’ was consistent. Lignin content showed a trend of rising. From 25 to 40 d after full blossom, ‘Zhipi’ and ‘Changshitou’ accumulated lignin slowly. The lignin content in ‘Zhipi’ was higher than in ‘Changshitou’ during this period. Rapid lignin accumulation started at different times. The rapid increase in lignin content in ‘Changshitou’ started around 40 days after full blossom, and it started from 55 d after full blossom in ‘Zhipi’. ‘Changshitou’ was thus 15 days earlier than ‘Zhipi’. At 55 d after full blossom, the lignin content in ‘Zhipi’ and ‘Changshitou’ rose rapidly, and in ‘Changshitou’, lignin content was higher than in ‘Zhipi’. During the endocarp development, cellulose content tended to rise in both varieties. At first, the cellulose content in ‘Zhipi’ was higher than in ‘Changshitou’. Starting around 35 d after full blossom, ‘Changshitou’ had a higher lignin content than ‘Zhipi’. The polyphenol content declined constantly. At first, it was higher in ‘Changshitou’, but from 45 d after full

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blossom, it declined faster in 'Changshitou' than in 'Zhipi'. The change patterns of C4H, CAD and PAL activities were similar. They displayed a downward trend after an initial rise. The enzyme activities in 'Zhipi' reached a peak at 55 d after full blossom, while those in 'Changshitou' at 70d after full blossom. From 25 to 70 d after full blossom, there were no significant differences between varieties. At 70 d after full blossom, the enzyme activities in 'Changshitou' were higher than in 'Zhipi'. The occurrence of the enzyme activity peak was coincide with the rapid accumulation of lignin. The study also found that the enzyme activity dropped to certain level, but rapid accumulation of lignin continued. The endocarp of the thick shelled 'Changshitou' had constantly significantly higher activities of POD and PPO than that of the thin shelled 'Zhipi', indicating that thicker endocarp needs to have higher the POD and PPO activities. In the whole process of endocarp development 'Changshitou' always had a higher PPO activity than 'Zhipi'. In, 'Zhipi' endocarp, lignin content and activity of CAD were significantly correlated, and cellulose content and PPO activity had a significant positive correlation during the early stage. During late period of rapid endocarp growth, lignin content was significantly and negatively correlated to C4H and CAD activities, and cellulose content had significant negative correlations with PPO, PAL, C4H and CAD activities, while polyphenol content and POD activity had a significant positive correlation. In 'Changshitou', during the early stage of endocarp development, a significant negative correlation was found between polyphenol and lignin contents; cellulose content was significantly positively correlated to PAL, C4H and CAD activities; and polyphenol content was significantly and negatively correlated to PAL and CAD activities. During the late period of rapid endocarp development, significant negative correlations were found between lignin content and PPO activity and between cellulose content and PPO activity.【Conclusion】Higher activities of PAL, CAD, C4H, PPO and POD as well abundant lignin precursors enables greater accumulation of lignin, which generates a thicker lignified endocarp as shown in the thick shelled 'Changshitou'.

Key words: Almond; Endocarp; Lignification; Enzyme activity

扁桃(*Amygdalus communis* L.)又名巴旦姆、巴旦木,是世界著名的坚果,具有很高的营养价值和经济价值^[1-2]。扁桃果实由外果皮、中果皮、内果皮与种仁组成,其内果皮和种仁是果实经济性状的重要组成部分,它们的品质也是评价一个扁桃品种优良与否的重要指标,如内果皮薄,出仁率高,价值高,反之则出仁率低,经济价值低^[2]。果实的内果皮是由子房壁的内表皮发育而来,由多层细胞经过木质化、厚壁化和石细胞化,最终形成硬核^[3-4]。

史梦雅等^[4]对桃内果皮发育的研究表明,桃内果皮的主要成分为木质素,木质素形成是一个快速的生理现象,在花后42~45 d,木质素开始在种尖部位沉积,然后从里向外进行木质化。郑志锋等^[5]对核桃内果皮发育的研究表明,核桃内果皮的主要成分为木质素和纤维素,且木质素含量高于纤维素。在内果皮木质化过程中木质素先后在细胞角隅、细胞间中形成,并进行各项生物合成活动,从而使次生细胞壁加厚,另一方面木质素能有效地和纤维素、半

纤维素连结,增加内果皮的稳定性和机械支持作用^[6]。因此内果皮的发育是一个复杂的过程,与木质素代谢等密切相关。木质素代谢过程中有很多酶参与,王丹阳^[7]和陶书田等^[8]对梨果实中石细胞形成进行研究,表明木质素代谢过程参与的酶有PAL、POD、PPO、C4H、CAD等,且木质素含量与这些酶均呈正相关。相关学者对桃^[9]和核桃^[10]内果皮木质素代谢相关酶活性进行研究表明木质化前期较高的PAL、POD活性开启了木质素的合成途径。

前人对木质素代谢及相关酶活性的报道多集中在梨果肉^[7-8]和部分核果类果树^[4,9-10],扁桃内果皮的薄厚与出仁率等品质性状紧密相关,但扁桃内果皮的形成与木质素关系及相关酶活性的变化等方面的研究还未见报道。本研究以‘纸皮’扁桃(薄壳)和‘长石头’扁桃(厚壳)两个品种为试材,分析了两个品种内果皮不同发育时期木质素含量以及相关酶活性变化,以期揭示内果皮发育与木质素关系的生理机制,为扁桃的品质育种提供理论依据。

1 材料和方法

1.1 试验材料

试验材料采于喀什地区莎车县新疆农业科学院园艺研究所扁桃种质资源保存圃,两个供试品种‘纸皮’(*Amygdalus communis* ‘Zhipi’)和‘长石头’(*Amygdalus communis* ‘Changshitou’),树龄均为40 a(年)。‘纸皮’内果皮(核壳)厚度约0.45 mm,‘长石头’内果皮厚度约4.55 mm。如图1,图2。



左. 纸皮;右. 长石头。 Left. Zhipi; Right. Changshitou.

图1 两个扁桃品种内果皮外观比较(花后115 d 成熟果)

Fig. 1 Comparison of endocarp appearance in two almond cultivars (ripe fruit at 115 days after full blossom)



左. 纸皮;右. 长石头。 Left. Zhipi; Right. Changshitou.

图2 两个扁桃品种果实横切内果皮间
苯三酚染液法^[4]染色结果(红色部分)

Fig. 2 Results of benzene triphenol staining^[4] in cross sections of fruits of the two almond cultivars

1.2 采样处理方法

分别选取薄壳‘纸皮’扁桃和厚壳‘长石头’扁桃各3株树作为试验采样株,作为3个生物学重复,于2016年4月25日(花后25 d)开始于每株采集发育正常果实20个混样,每隔15 d采样1次,至果实成熟为止,共计7次(采样时间分别为花后25、40、55、70、85、100、115 d)。采样后立即带回实验室,去除种仁

和外果皮,留取内果皮液氮中保存待用。

1.3 测试指标及方法

木质素含量测定参照陶书田等^[8]巯基乙酸法,纤维素含量的测定采用72%H₂SO₄酸解洗涤法^[11],酚类物质含量测定采用Folin-ciocalteu法^[12-13]并稍加改进:提取方法不变,反应液为1 mL提取液,福林酚0.4 mL,10%碳酸钠0.8 mL,定容至10 mL,25 ℃水浴60 min,然后于765 nm比色,以蒸馏水调零。3次重复。PAL活性测定参照刘小阳等^[14]和Duan等^[15]的方法,POD活性测定参照愈创木酚法^[16-17],PPO活性按Quan等^[18]方法测定,CAD的提取和活性测定参照Wróbel-kwiatkowska等^[19]的方法进行,C4H活性的测定参照金丽萍等^[20]和Salvador等^[21]的方法。

采用Excel 2010软件进行数据统计和图表绘制,SPSS 20.0软件进行相关性分析。

2 结果与分析

2.1 扁桃果实不同发育时期内果皮木质素、纤维素含量的变化

对‘纸皮’和‘长石头’扁桃花后25~115 d内果皮中的木质素和纤维素含量进行测定,结果如图3所示。结果表明,两个品种的木质素含量在花后25~

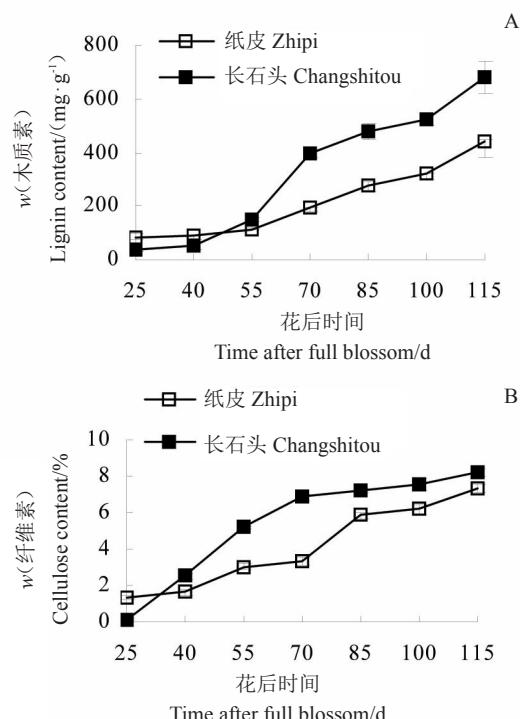


图3 两个扁桃品种不同发育时期内果皮木质素及纤维素含量的变化

Fig. 3 Changes in lignin and cellulose contents in different development periods in the two almond varieties

55 d 变化差异不大,花后 55~70 d ‘长石头’扁桃内果皮木质素含量迅速上升,显著高于‘纸皮’扁桃,且这种差距一直持续到花后 115 d(图 3-A)。两个扁桃品种的纤维素含量变化趋势与木质素基本一致,在花后 25 d ‘纸皮’扁桃内果皮的纤维素含量略高于‘长石头’扁桃,但到花后 40 d 开始‘纸皮’扁桃内果皮的纤维素含量明显低于‘长石头’扁桃,并且这种差距在花后 70 d 达到最大,到花后 115 d ‘纸皮’扁桃内果皮的纤维素含量依然低于‘长石头’扁桃(图 3-B)。

2.2 扁桃果实不同发育时期内果皮酚类物质含量的变化

对‘纸皮’和‘长石头’扁桃花后 25~115 d 内果皮中的酚类物质含量进行测定,结果如图 4 所示。两个扁桃品种内果皮中酚类物质含量在果实发育过程中均呈现逐渐下降的趋势,在花后 25~40 d ‘纸皮’扁桃内果皮中的酚类物质含量低于‘长石头’扁桃,但自花后 55 d 开始‘纸皮’扁桃内果皮的酚类物质含量持续高于‘长石头’扁桃。

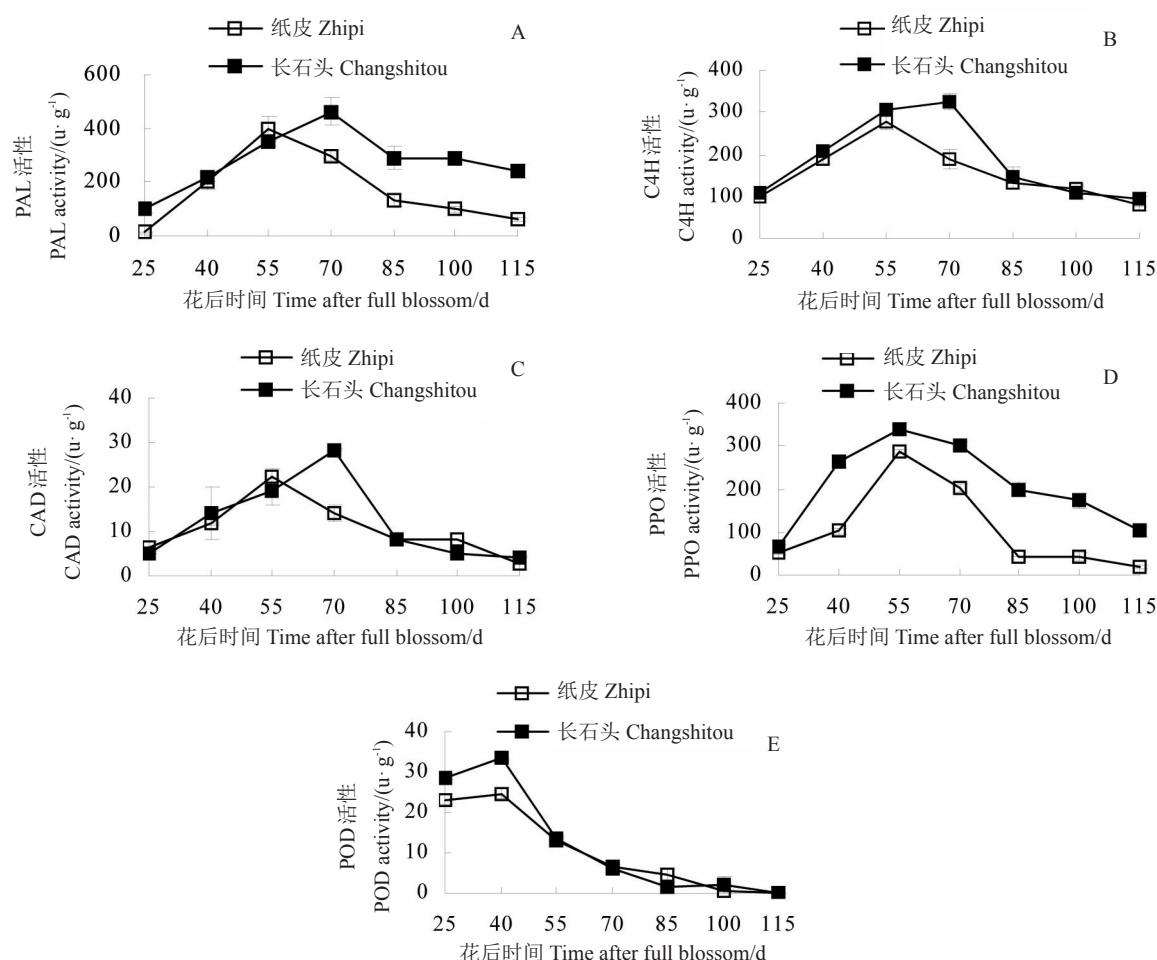


图 4 两个扁桃品种不同发育时期内果皮酚类物质含量的变化

Fig. 4 Changes in polyphenol content in different development periods in the two almond varieties

2.3 扁桃内果皮木质素合成相关酶活性的变化

对‘纸皮’和‘长石头’扁桃花后 25~115 d 内果皮中的 PPO、POD、PAL、C4H、CAD 酶活进行测定结果如图 5 所示。PAL 酶活性在‘纸皮’和‘长石头’扁桃之间均呈现先上升后下降的趋势,在花后 25~55 d 的上升阶段两个品种之间几乎没有差异,

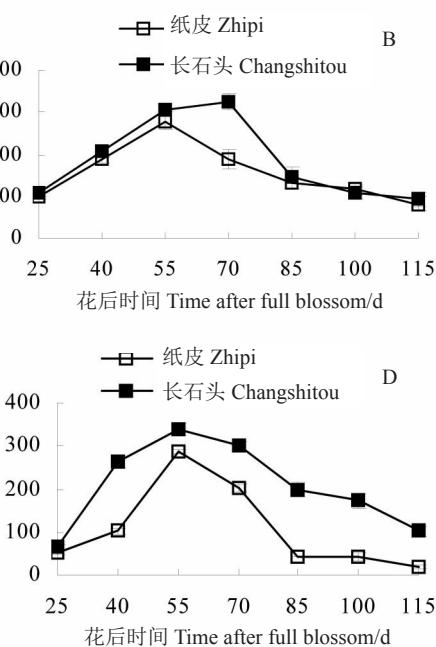


图 5 两个扁桃品种不同发育时期内果皮相关酶活性的变化

Fig. 5 Changes in related enzyme activities in the endocarp of the two almond varieties during fruit development

但在花后 55~115 d ‘长石头’扁桃的 PAL 酶活性始终高于‘纸皮’扁桃(图 5-A);C4H 酶活性在‘纸皮’和‘长石头’扁桃之间均呈现先上升后下降的趋势,花后 25~55 d 和 85~115 d 两品种之间几乎没有差异,但在花后 55~85 d 期间‘长石头’扁桃的 C4H 酶活性明显高于‘纸皮’扁桃(图 5-B);CAD 酶活性变化与 C4H 酶相似,在花后 25~55 d 和 85~115 d 两个品种之间几乎没有差异,但在花后 70 d 时‘长石头’扁桃明显高于‘纸皮’扁桃(图 5-C);PPO 酶活性在‘纸皮’和‘长石头’扁桃之间均呈现先上升后下降的趋势,并且在花后 25 d 之后一直到采收‘长石头’的 PPO 酶活性都明显高于‘纸皮’扁桃(图 5-D);POD 酶活性在花后 25~40 d 时‘长石头’高于‘纸皮’扁桃,但随后从花后 55~115 d 两个品种之间几

乎没有差异(图 5-E)。

2.4 扁桃内果皮主要成分与相关酶活性变化相关性分析

对扁桃果实内果皮发育过程中 PPO、POD、PAL、C4H、CAD 活性与内果皮主要成分木质素、纤维素、酚类物质进行相关性分析,结果表明,‘纸皮’扁桃内果皮快速发育前期木质素含量与 CAD 活性显著正相关($r=0.999^*$),而纤维素含量则与 PPO 活性显著正相关,($r=1.000^*$);内果皮快速发育后期木质素含量与 C4H、CAD 活性呈显著负相关,($r=-0.976^*, -0.978^*$),纤维素含量与 PPO、PAL、C4H、CAD 活性呈显著负相关,($r=-0.970^*, -0.993^*, -0.990^*, -0.974^*$),酚类物质与 POD 活性显著正相关,($r=0.963^*$)(详见表 1)。

表 1 两个扁桃品种内果皮相关成分与木质素相关酶活性的相关性分析
Table 1 Correlation analysis of the main components with lignin-related enzymes activities
in the endocarp of the two almond varieties

| 木质素 Lignin | 纤维素 Cellulose | 酚类物质 Polyphenol | PPO | POD | PAL | C4H | CAD | 时期 Stage | 品种 Variety | 成分 Composition |
|---------------|------------------|--------------------|---------|----------|----------|---------|---------|---------------------|--------------------|--------------------|
| 1 | 0.981 | 0.390 | 0.985 | -0.883 | 0.989 | 0.989 | 0.999* | 前期 Earlier stage | 纸皮 Zhipi | 木质素 Lignin |
| | 0.940 | -0.797 | -0.831 | -0.881 | -0.902 | -0.976* | -0.978* | 后期 Late stage | | |
| | 0.881 | -0.965* | 0.533 | -0.951 | 0.949 | 0.949 | 0.992 | 前期 Earlier stage | 长石头 Changshitou | |
| | 0.993 | -0.640 | -0.998* | -0.787 | -0.975 | -0.890 | -0.813 | 后期 Late stage | | |
| 1 | 0.559 | 1.000* | -0.957 | 0.943 | 0.943 | 0.989 | 0.989 | 前期 Earlier stage | 纸皮 Zhipi | 纤维素 Cellulose |
| | -0.726 | -0.970* | -0.877 | -0.993** | -0.990** | -0.974* | -0.974* | 后期 Late stage | | |
| | -0.948 | 0.862 | -0.883 | 0.997** | 0.987* | 0.983* | 0.983* | 前期 Earlier stage | 长石头 Changshitou | |
| | -0.724 | -0.998* | -0.710 | -0.942 | -0.937 | -0.875 | -0.875 | 后期 Late stage | | |
| 1 | 0.543 | -0.776 | 0.251 | 0.251 | 0.430 | 0.430 | 0.430 | 前期 Earlier stage | 纸皮 Zhipi | 酚类物质 Polyphenol |
| | 0.593 | 0.963* | 0.730 | 0.788 | 0.686 | 0.686 | 0.686 | 后期 Late stage | | |
| | -0.713 | 0.846 | -0.967* | -0.889 | -0.988* | -0.988* | -0.988* | 前期 Earlier stage | 长石头 Changshitou | |
| | 0.682 | 0.028 | 0.452 | 0.920 | 0.967 | 0.967 | 0.967 | 后期 Late stage | | |

注: **. 在 0.01 水平(双侧)上显著相关, *. 在 0.05 水平(双侧)上显著相关。

Note: ** Correlation is significant at the 0.01 level, * Correlation is significant at the 0.05 level.

‘长石头’扁桃内果皮快速发育前期木质素含量与酚类物质呈显著负相关,($r=-0.965^*$);纤维素含量与 PAL、C4H、CAD 显著正相关,($r=0.997^*, 0.987^*, 0.983^*$);酚类物质与 PAL、CAD 活性呈显著负相关,($r=-0.967^*, -0.988^*$);内果皮快速发育后期木质素含量与 PPO 活性呈显著负相关($r=-0.998^*$),纤维素含量与 PPO 活性显著负相关($r=-0.998^*$)。

扁桃果实内果皮整个发育过程中,木质素含量与纤维素呈正相关,与酚类物质呈负相关,与 POD 活性呈负相关。

3 讨 论

内果皮是细胞次生壁形成及增厚并不断木质化的过程,且木质素和纤维素含量的积累表明木质化程度的高低^[10]。有研究表明内果皮木质化过程中木质素先后沉积在细胞角隅、细胞间隙、初生壁和次生壁中,进而与纤维素、半纤维素连接,对骨架起到填充作用,在这期间伴随着细胞层数的逐渐增加,木质素逐渐积累^[10,22],因此,推测木质素的沉积与内果皮木质化加厚密切相关。本研究通过对扁桃内果皮相

关生理指标的测定,结果显示,两个扁桃品种内果皮发育过程中木质素含量与纤维素含量呈正相关,均呈现上升趋势,这与朱秋萍等^[22]的组织解剖学研究中内果皮木质素沉积观察情况相符。还发现‘长石头’在花后55 d之后,其内果皮的木质素含量明显高于‘纸皮’扁桃,并且纤维素含量在花后40 d之后也高于‘纸皮’扁桃,推测‘长石头’扁桃之所以壳厚可能与内果皮的木质素和纤维素积累量较‘纸皮’高有关。本研究发现两个扁桃品种内果皮中木质素含量均高于纤维素含量,这与郑志锋等^[5]研究核桃结果一致,进一步证实了扁桃木质素沉积是内果皮木质化增厚的关键因素。

酚类物质是木质素特异合成产物的重要前体物质^[23],本研究结果显示,酚类物质含量与木质素、纤维素含量变化趋势相反,‘纸皮’和‘长石头’木质素含量分别在花后55 d和40 d迅速积累,两个扁桃品种酚类物质含量则在迅速下降,内果皮快速发育后期‘长石头’酚类物质消耗量大于‘纸皮’,且木质素含量积累量高于‘纸皮’,这可能是因为厚壳扁桃品种需要大量酚类物质作为木质素合成前体物质。本研究相关分析显示,木质素的积累与酚类物质含量的变化呈显著负相关,这与刘国强等^[24]研究一致,进一步证实了酚类物质与木质素合成的前体物质密切相关,其充分积累有利于后期内果皮木质素成分的积累,促使内果皮完成木质化进程。

在木质素形成过程中有多种多样的酶参与,人们广泛认为苯丙烷代谢形成木质素单体及脱氢羟化聚合形成成熟的木质素过程最为关键^[25-27]。在这两个途径中分别有大量的酶参与,PAL、C4H等是苯丙烷代谢途径的关键酶^[28-29];而在木质素合成的特异途径中的关键酶有:PPO、POD和CAD等^[26,28,30]。PAL是木质素单体生物合成过程中涉及的第一个酶,是苯丙烷代谢途径中的限速酶,而C4H是苯丙氨酸代谢途径的第二步,是木质素单体形成过程中的重要酶,它们在一定程度上能体现木质素的代谢情况。本研究发现两扁桃品种PAL和C4H活性均呈现先升高后下降的趋势,‘纸皮’(花后55 d)和‘长石头’(花后70 d)PAL和C4H活性达到高峰后木质素才开始大量积累,酶活性达到高峰之后活性和高峰值‘长石头’均高于‘纸皮’,这些也表明了内果皮需要PAL、C4H活性达到相对较高水平时木质素才能大量积累,这与曹爱娟等^[9]研究桃结果相同,本研究还

发现PAL、C4H活性达到高峰后厚壳‘长石头’对PAL、C4H活性高于薄壳‘纸皮’,曹爱娟等^[9]研究两个桃品种PAL、C4H活性差异不明显,这是由于这两个桃品种厚薄程度差异不大,因此,推测PAL、C4H活性高低与扁桃内果皮厚薄有着密切的关系。PPO可催化酚类物质合成木质素所需要的前体物质。本研究发现两个扁桃品种PPO活性均呈现先上升后下降,且厚壳‘长石头’PPO活性始终高于‘纸皮’,进一步证实了厚壳‘长石头’扁桃需要较高的PPO酶活性催化形成大量酚类物质作为木质素合成前体物质来积累木质素,从而促使内果皮木质化加厚。木质素单体合成的最后阶段是由CAD将香豆醛、松柏醛、芥子醛催化分别形成香豆醇、松柏醇、芥子醇。本研究结果CAD活性呈现先上升后下降趋势,且高峰值‘长石头’高于‘纸皮’,认为CAD活性达到较高水平,木质素才能大量积累,研究结果与曹爱娟等^[9]研究结果一致。POD活性参与植物活性氧代谢中的一类重要的酶,同时也是木质素合成途径中最后一步起着关键作用的酶。本研究表明POD活性与木质素、纤维素、酚类物质含量呈现显著负相关,与文菁等^[10]研究结果一致。而前人研究山竹果实^[31]和南瓜^[32]受机械损伤后,结果表明POD活性增强,促进了木质素的积累,组织的木质化程度增强,这可能是由于果实品种不同,其内物质相互转换差异的原因所致。木质素的合成是一个非常复杂的生物化学过程,除了这些酶还有其他酶反应和非酶反应的参与,本研究还发现酶活性下降到一定水平时,但木质素仍在大量积累,这可能与非酶反应有关,不同酶在扁桃内果皮发育过程中所起的作用可能不同。

本研究发现‘长石头’在扁桃内果皮木质化过程中PAL、CAD、C4H、PPO、POD活性高峰值均明显高于‘纸皮’扁桃,且两个品种PAL、CAD、C4H、PPO、POD活性扁桃趋势相同,均呈现先上升后下降趋势,酶活性达到高峰之后逐渐降低的原因可能是由于木质素的积累抑制了酶的活性有待下一步研究。在扁桃内果皮木质化过程中还有很多非酶类和酶类物质参与反应,这些具体在扁桃内果皮木质素代谢中起着什么作用也待于进一步研究。

4 结 论

薄壳‘纸皮’和厚壳‘长石头’两个品种在木质素

积累、纤维素与酚类物质含量方面存在差异;两个品种木质素、纤维素含量均在积累,‘长石头’扁桃内果皮的木质素和纤维素含量分别在花后55 d和40 d起始终高于‘纸皮’扁桃,但酚类物质在逐渐消耗且‘长石头’内果皮的酚类物质含量始终低于‘纸皮’扁桃;‘长石头’在扁桃内果皮木质化过程中PAL、CAD、C4H、PPO、POD活性高峰值均明显高于‘纸皮’扁桃,‘长石头’PAL和PPO活性后期均高于‘纸皮’,相关性分析表明,扁桃内果皮木质素含量与纤维素呈正相关关系,而与酚类物质含量呈负相关关系,与木质素快速积累后期PAL、CAD、C4H、PPO、POD活性呈负相关。由此认为,当PAL、C4H、CAD、PPO、POD活性到达到一个相对较高水平时形成木质素合成所需的前体物质之后扁桃内果皮才能够快速大量积累木质素,从而使内果皮木质化加厚。

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