

杭州和泰安甜樱桃不同发育阶段花芽内含物及花芽质量的比较研究

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摘要:【目的】比较杭州和泰安地区甜樱桃在休眠前、休眠中、花芽萌动前花芽内营养物质含量与内源激素水平差异, 对花芽萌动前两地区甜樱桃花芽内含物及其与花芽质量相关的综合分析, 从生理水平揭示杭州地区花芽发育质量较低的原因。【方法】以低温需冷量不同的2个甜樱桃品种为试材, 比较杭州和泰安地区相同甜樱桃品种在不同发育阶段花芽内含物水平差异, 对花芽萌动前甜樱桃花芽内含物进行主成分分析与花芽形态指标、花器官发育质量进行相关性分析。【结果】两地区甜樱桃在不同发育阶段花芽内含物有较大差异。杭州地区甜樱桃在进入休眠后花芽内淀粉、可溶性蛋白含量先大量增加后下降, 还原糖含量基本稳定, 泰安地区甜樱桃花芽内可溶性蛋白含量增加。在花芽萌动前, 泰安甜樱桃(TS、TB)花芽内可溶性蛋白含量分别为杭州甜樱桃(HS、HB)的1.16、1.13倍, 还原糖含量分别是其的2.00、1.59倍。主成分分析表明, 在花芽萌动前, 泰安地区甜樱桃花芽内含物水平较高。相关性分析表明, 花芽萌动前花芽内含物水平与花芽大小及后期花器官发育质量相关。【结论】花芽萌动前, 杭州地区甜樱桃花芽内营养物质贮备较不充足, 其内含物水平偏低, 尤其是可溶性蛋白、还原糖含量较低, 使后期花器官发育质量均受到一定影响。

关键词: 甜樱桃; 营养物质; 内源激素; 花器官发育质量; 杭州; 泰安

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Comparative study on flower bud inclusion and quality in different development stages of sweet cherry from Hangzhou and Tai'an

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Abstract: 【Objective】Sweet cherry is the earliest ripening fruit in north China and mainly cultivated in Tai'an, Yantai and Dalian. South China becomes warm earlier and faster in spring than the north, so it can be earlier for marketing. Besides, sweet cherry cultivation has gradually expanded to the south due to the leisure picking market's promoting in recent ten years. However, the introduction of sweet cherry to south is not succeeded because of the low fruiting rate, poor fruiting habits and fruit malformation. Previous studies showed that these phenomena were related to the flower organ development. Flower bud differentiation is a morphogenetic process as well as a physiological and biochemical process. The physiological differentiation of flower bud is on the basis of accumulation and synergistic effect of nutrients and endogenous hormones. Therefore, the development quality of flower bud is closely related to the accumulation of nutrients and endogenous hormones in trees. In this study, the differences in nutrient contents and endogenous hormone levels in flower buds during three stages (before dormancy, during dormancy and before budbreak) of the same sweet cherry varieties in Hangzhou and Tai'an were compared, the correlation between flower bud quality and flower bud inclusion before bud break were analyzed, in order to reveal the physiological reasons for the low quality of flower bud in Hangzhou ar-

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ea and provide the theoretical basis for the formulating reasonable cultivation and management measures, which can be used for regulating growth and developments, and achieving stable and high yield in the future. **【Methods】**Five years old sweet cherry trees in Hangzhou and Tai'an were used as the experimental materials. Two cultivars of sweet cherry with different chilling requirement were chosen in this study. Firstly the leaf fall and budbreak periods of two cultivars in two areas were recorded. Then, more than 30 buds from each cultivar were collected during three stages, before dormancy, during dormancy and before budbreak. The nutrient indices (such as starch content, total soluble sugar content, soluble protein content, reducing sugar content and free amino content) and endogenous hormones indices (such as GA₃, IAA, ABA and ZR_s) were determined at three stages. The flower bud index (such as longitudinal diameter, transverse diameter and weight) before budbreak and the floral organ quality parameters (such as the length of pistil and stamen, average number of flowers per cluster, diameter of ovary, stamen numbers and the embryo sac abortion rate) were investigated. Finally, multiple indicators were analyzed using the correlation analysis method and principal component analysis. **【Results】**The results revealed that after entering dormancy, the starch, soluble sugar and protein contents in flower bud of two sweet cherry varieties in Hangzhou area increased greatly, it reached the peak value at the stage of "during dormancy", then decreased gradually, in which the total content of soluble sugar decreased greatly. While the reducing sugar and free amino acid contents changed little during these three stages, their contents were basically stable. Meanwhile, the contents of soluble sugar, reducing sugar and soluble amino acid in flower bud of two sweet cherry varieties in Tai'an area increased greatly, but the starch content decreased rapidly. From the stage of "during dormancy" to "before budbreak", these four indices all dropped gradually, and the contents of reducing sugar, soluble amino acid and sugar dropped a lot. However, the content of soluble protein increased a little, and its content was basically stable. The study also revealed that the endogenous hormone contents in flower bud in two areas at three stages had the same trend except for ABA. But the absolute amount of a single endogenous hormone just represented the metabolic level of the hormone at one stage, while the interaction between multiple hormones affected the entire dormancy process. Before budbreak, the ratios of ZR_s/GA, ZR_s/IAA, ABA/IAA, ABA/GA and IAA/GA with HS were 0.31, 0.41, 3.31, 2.47 and 0.75, respectively. The ratios with HB were 0.28, 0.31, 2.72, 2.40 and 0.88, respectively. The ratios with TS were 0.31, 0.29, 1.7, 1.8 and 1.06, respectively. The ratios with HB were 0.34, 0.25, 1.46, 1.98 and 1.35, respectively. Obviously, the ratios of ZR_s/GA and IAA/GA were lower than those in Tai'an area. Principle component analysis showed that the inclusions in flower bud before budbreak were TS > TB > HS > HB. The correlation analysis of the 9 indices with flower bud index displayed that at the stage of "before budbreak", the content of soluble protein was positively correlated with reducing sugar, the content of starch was positively correlated with ABA but negatively correlated with soluble amino acid and IAA. The content of soluble amino acid was positively correlated with IAA but negatively correlated with ABA. The longitudinal diameter of flower bud was negatively correlated with the contents of starch and ABA but positively correlated with the contents of soluble amino acid and IAA. The transverse diameter of flower bud was negatively correlated with ZR_s. The weight of flower bud was positively correlated with the content of reducing sugar. The correlation analysis of 9 indices with flower organ quality displayed that at the stage before flower bud initiation, the embryo sac abortion rate was negatively correlated with the soluble protein content but positively correlated with starch content. In conclusion, the contents of nutrients and endogenous hormones before flower bud initiation were closely related to the size of flower bud and the quality of flower organ development at later stage. **【Conclusion】**It was obviously suggested that the storage of nutrients in flower buds before budbreak in Hangzhou area was insufficient, and the overall level was low,

especially the contents of soluble protein and reducing sugar was low, but the starch content was high, which should be the physiological reason for the low quality of flower organs in this area. Whereas with the further differentiation of flower organs after bud initiation, a series of dynamic changes of nutrient composition and endogenous hormone content still appeared, and whether this stage was more correlated with the quality of flower bud development needed further study.

Key words: Sweet cherry; Nutrient; Endogenous hormone; Flower organ quality; Hangzhou; Tai'an

甜樱桃(*Prunus avium* L.)俗称大樱桃,是我国北方成熟最早的落叶果树,集中栽培于泰安、烟台、大连等地。近年来,受其较高的种植效益及市场潜力的驱动,逐渐向南方地区扩展,如长江中下游的江浙沪长三角暖湿地区。目前南方地区甜樱桃引种试栽过程中存在坐果率低等问题,其中花芽发育异常为其主要问题,已有研究表明南方地区甜樱桃雌雄配子体发育异常、花器官发育质量较差是其坐果率低、结实困难的主要原因^[1-2]。

花芽发育在形态建成过程中伴随着生理生化方面一系列的变化。花芽生理分化是营养物质、激素等多方面积累、协同作用,从量变到质变的过程,是形态分化的物质基础。橄榄在花芽形态分化过程中,淀粉在花芽内大量积累^[3]。对红富士苹果研究表明,碳水化合物虽对花芽分化的启动影响不大,但与后期形成的花芽质量密切相关,较高的淀粉含量和C/N比形成的花芽更为饱满^[4]。杨梅在生理分化前可溶性糖含量对花芽分化率密切相关^[5]。樊卫国等^[6]研究表明,刺梨花芽分化期需要高水平的ZR₅和碳水化合物,但对GA₁₊₃、IAA、ABA则需求较低。甜樱桃花芽分化分为两个阶段,在当年生长季完成各个器官原基的分化,于翌年春季进一步发育形成成熟花器官。王玉华等^[7]研究发现,甜樱桃在当年生长季的花芽分化期需要高水平的ZR₅和低水平的GA₁₊₃、IAA。ZR₅/IAA、ZR₅/GA₁₊₃、ABA/IAA、ABA/GA₁₊₃值较高更有利于花芽形成。职倩倩等^[8]通过多糖定位研究表明,在春季花器官发育期间,高温环境抑制了淀粉等多糖水解间接引起胚囊的败育。由前人的研究结果可知,花芽分化与树体内营养物质及内源激素水平密切相关。

笔者课题组前期对杭州和泰安两地区甜樱桃花芽发育研究表明,两地区甜樱桃花芽发育质量差异重点表现在花器官发育阶段雌雄配子体出现异常^[9]。目前,前人已经阐明该阶段雌雄配子体发育过程中的异常,但对引起其异常的生理原因并未分析。甜樱桃作为“先花后叶型”果树,春季的花器官

分化发育依赖于上一季积累的能量物质,其甜樱桃休眠前、花器官发育前等时期花芽内营养物质含量与内源激素水平及其与整体花器官质量的关系尚未见报道。因此研究杭州地区甜樱桃不同发育阶段尤其是花芽萌动花器官发育前,花芽内营养积累情况、内源激素水平及其与整体花器官发育质量的关系,对从生理层面揭示花芽发育质量较低的原因具有指导意义。笔者以此为切入点,选取2个不同需冷量甜樱桃品种为试材,分别测定了杭州和泰安两地区甜樱桃花芽休眠前、休眠中及花芽萌动前的营养物质含量及内源激素水平,探究两地区相同品种甜樱桃花芽在同一发育时期的营养和内源激素水平差异及其与花器官质量的相关性,以期从生理生化水平揭示两地区花芽发育质量差异的原因,为今后杭州地区及类似生境区域甜樱桃种植制定合理的增产措施、调控其生长发育、达到稳产优产提供理论依据。

1 材料和方法

1.1 试验材料

试验材料分别种植于浙江杭州转塘街道甜樱桃研究基地(北纬30°9'34",东经120°4'37")、山东泰安高新区红旗樱桃合作社种植基地(北纬36°11'07",东经117°06'51"),2个供试品种为萨米脱(Summit)、布鲁克斯(Brooks),树龄均为5 a,分别以杭州萨米脱(HS)、杭州布鲁克斯(HB)、泰安萨米脱(TS)、泰安布鲁克斯(TB)编号各地区品种。

1.2 采样处理方法

2019年10月—2020年3月,在前期连续2 a观察两地2个甜樱桃品种落叶期与萌芽期基础上,于休眠前(完全落叶1月前)、休眠中(完全落叶1月后)、花芽萌动前(花芽刚露红时)3个阶段分别采集2个品种花芽数十个,立即置于液氮中冷冻并带回实验室置于-80℃冰箱中待测。具体采样时间分别为:杭州地区2019-11-29、2020-02-09、2020-02-27;泰安地区2019-10-31、2020-01-13、2020-03-06。

1.3 测定指标及方法

测定花芽内源激素的方法:采用中国农业大学提供的ELISA试剂盒,测定赤霉素(GA₃)、生长素(IAA)、脱落酸(ABA)、玉米素核苷(ZR₅)含量。样品中内源激素通过80%甲醇提取,使用Waters公司C₁₈固相萃取柱,每个参数设有生物学3次重复。

测定花芽内碳水化合物及其他参数的方法:淀粉、可溶性糖含量采用蒽酮法测定。还原糖含量采用3,5-二硝基水杨酸比色法测定。可溶性蛋白含量采用考马斯亮蓝G-250法测定。游离氨基酸含量采用茚三酮法测定。每个参数设有生物学3次重复。

花芽形态指标的测定:于花芽萌动前采集每个

品种花芽10个用游标卡尺测量记录每个品种的花芽纵横径、采集每个品种花芽20个称取质量。

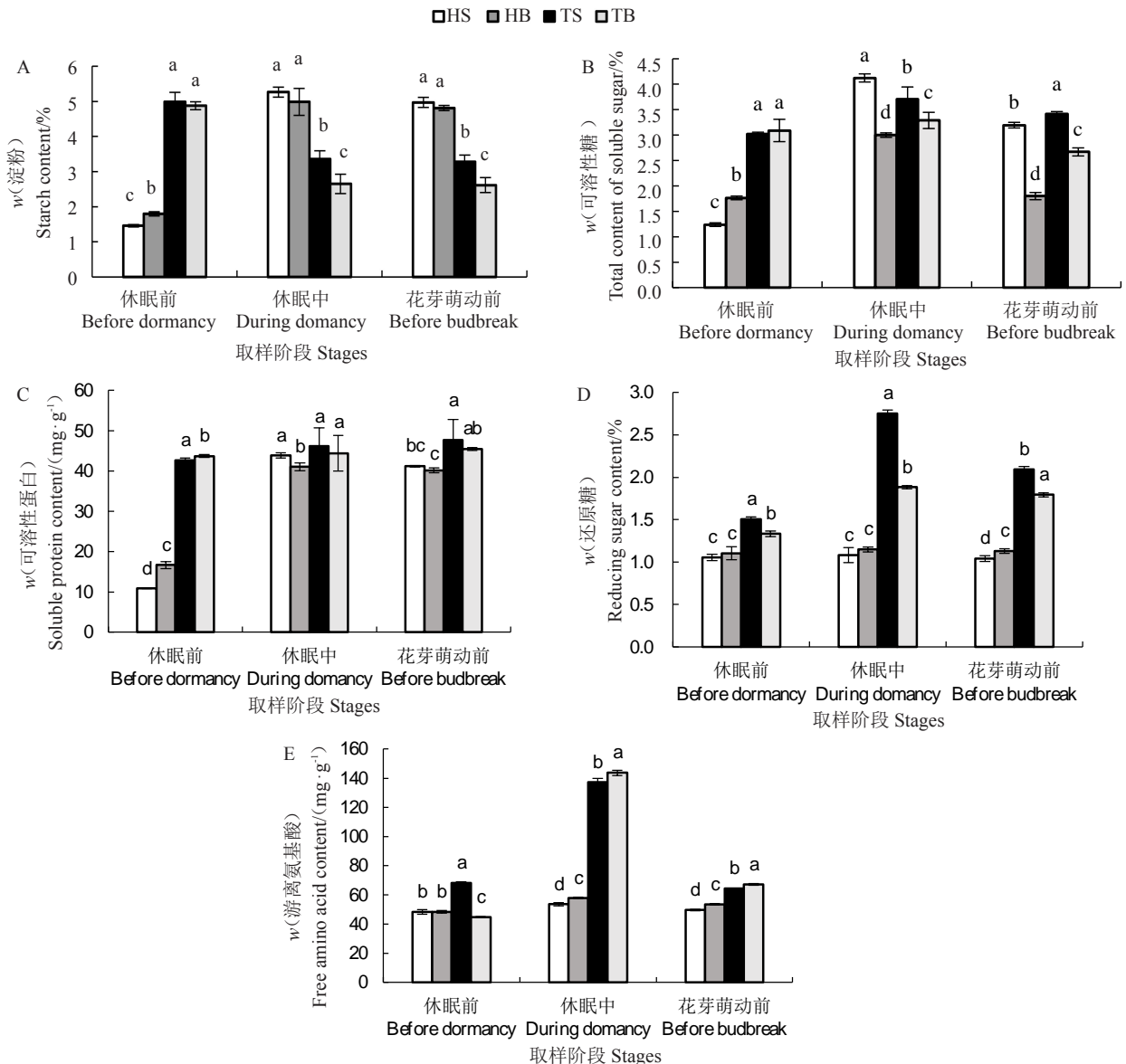
花器官质量的测定:于花期采集每个品种盛开花朵15枚用游标卡尺测量记录每个品种的雌雄蕊长度、子房直径、雄蕊数目等指标。

采用Excel 2016和DPS 18.10软件对数据进行统计分析,采用单因素方差分析和Duncan法比较差异显著水平($p < 0.05$)。

2 结果与分析

2.1 两地区不同阶段甜樱桃花芽营养物质含量比较

由图1可知,在休眠前,杭州地区2个甜樱桃品



不同小写字母表示差异显著($p < 0.05$)。下同。

Different small letters means significant difference at $p < 0.05$. The same below.

图1 两地区不同阶段甜樱桃花芽营养物质含量的比较

Fig. 1 Comparison of nutrient contents in flower buds of sweet cherry at different stages in two regions

种花芽内淀粉含量显著低于泰安地区,进入休眠后,杭州地区甜樱花芽内淀粉含量迅速增加,而此时泰安地区甜樱桃则呈相反变化趋势,表现为花芽内淀粉含量下降。在休眠中期,泰安地区2个甜樱桃品种花芽内淀粉含量显著低于杭州地区。休眠中至花芽萌动前,两地区甜樱花芽内淀粉含量均有略微降低(图1-A)。

在休眠前,杭州地区2个甜樱桃品种花芽内可溶性糖含量显著低于泰安地区。进入休眠后,两地区甜樱花芽内可溶性糖含量逐渐增加,杭州地区2个甜樱桃品种花芽内可溶性糖含量增加量较大,HS、HB分别比休眠前增加了2.18%、0.70%,此时HS和TS之间并无显著差异。在花芽萌动前,两地区甜樱花芽内可溶性糖含量降低,杭州地区2个甜樱桃品种花芽内可溶性糖含量显著低于泰安地区(图1-B)。

图1-C表明,休眠前至休眠中期,甜樱花芽内可溶性蛋白含量均呈升高趋势,杭州地区增加量较大,在休眠中期,HS花芽内可溶性蛋白含量是休眠前的4.03倍,HB为2.46倍,说明此时杭州地区2个甜樱桃品种花芽内可溶性蛋白大量增加,并进一步积累贮存。TS、TB增加量较少,为休眠前的1.08倍、1.02倍。休眠中向花芽萌动转化时期,HS、HB花芽内可溶性蛋白含量少量降低,此时TS、TB花芽内可溶性蛋白含量依然有少量增加。

两地区甜樱花芽内还原糖含量在进入休眠后也出现显著差异,泰安地区甜樱花芽内还原糖含量大幅上升,杭州地区甜樱花芽内还原糖含量增加量较少,HS、HB仅比休眠前增加了0.03%、0.04%。花芽萌动前,泰安地区甜樱花芽内还原糖含量明显下降,杭州地区甜樱花芽内还原糖含量略微下降。在3个阶段中,杭州地区2个甜樱桃品种花芽内还原糖含量变化较为平稳,均显著低于泰安地区(图1-D),由此可见,还原糖可能不是杭州地区甜樱桃休眠时花芽内主要的储能物质。

与还原糖含量变化趋势相同,在3个阶段中杭州地区2个甜樱桃品种花芽内游离氨基酸含量变化总体也较为平稳。而泰安地区2个甜樱桃品种在进入休眠后,花芽内游离氨基酸含量急剧上升,于花芽萌动前迅速下降(图1-E)。

综合图1可知,在不同阶段,两地区甜樱花芽内营养物质代谢情况有所不同:进入休眠后,杭州地区2个甜樱桃品种花芽内淀粉、可溶性糖、可溶性蛋

白含量大量增加,在休眠中期到达峰值,随后逐渐下降,其中可溶性糖含量降幅较大,而自休眠前至花芽萌动前还原糖和游离氨基酸变化较小,其含量基本稳定。

泰安地区2个甜樱桃品种在进入休眠后,可溶性糖、还原糖、游离氨基酸含量大量增加,淀粉含量则迅速下降,从休眠中至花芽萌动前,淀粉、还原糖、游离氨基酸、可溶性糖含量逐渐下降,其中还原糖、游离氨基酸、可溶性糖含量降幅较大,自休眠前至花芽萌动前可溶性蛋白含量虽有所增加但变化较小,其含量基本稳定。

2.2 两地区不同阶段甜樱花芽内源激素含量的比较

由图2-A可知,从休眠前至花芽萌动前,甜樱花芽内GA₃含量呈逐渐升高趋势。在进入休眠前,TS花芽内GA₃含量显著高于HS,进入休眠后HS花芽内GA₃含量升高,HS和TS之间差异不显著,花芽萌动前HS花芽内GA₃含量已高于TS。HB花芽内GA₃含量在休眠中显著高于TB,花芽萌动前,HS花芽内GA₃含量仍高于TS。由此可知,随着休眠阶段花芽内GA₃含量的升高积累,于花芽萌动前,杭州地区2个甜樱桃品种花芽内GA₃含量均高于泰安地区。

进入休眠后,甜樱花芽内IAA含量则呈不同的变化趋势。在进入休眠前,泰安地区甜樱花芽中IAA含量高于杭州地区,此时TS显著高于HS。进入休眠后花芽内IAA含量的增加,杭州地区甜樱花芽中IAA含量明显高于泰安地区,其中HB和TB之间差异最显著。休眠中至花芽萌动前,甜樱花芽内IAA含量逐渐降低,杭州地区2个甜樱桃品种花芽内IAA含量均显著低于泰安地区(图2-B)。

图2-C表明,在进入休眠前,杭州地区甜樱花芽中ABA含量显著高于泰安地区。从进入休眠至花芽萌动前,两地区甜樱花芽内ABA含量变化差异显著。杭州地区2个甜樱桃品种花芽内ABA含量呈先降低后升高的趋势,而泰安地区两品种则呈不同的变化趋势,TS、TB花芽内ABA含量有所增加,在花芽萌动前则大幅下降。在休眠中和花芽萌动前,两地区花芽内ABA含量差异显著。

从图2-D可知,从进入休眠至花芽萌动前,甜樱花芽内ZR_s含量呈“V”形变化趋势。在进入休眠前,杭州地区2个甜樱桃品种花芽内ZR_s含量均高于泰安地区,进入休眠后,花芽内ZR_s含量降低,其中

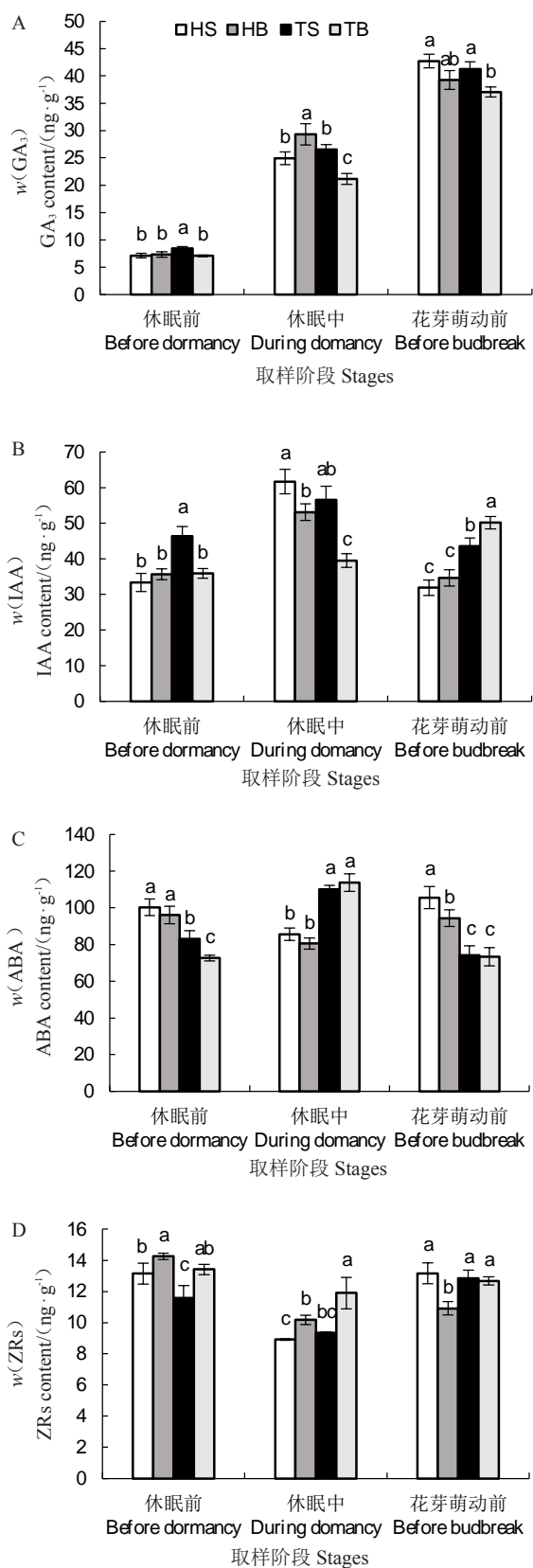


图2 两地区不同阶段甜樱桃花芽内源激素含量的比较
 Fig. 2 Comparison of endogenous hormone contents in flower buds of sweet cherry at different stages in two regions

HB花芽内ZRs含量显著低于TB。直至花芽萌动前,HS花芽内ZRs含量较高于TS,而HB花芽内ZRs含量仍显著低于TB。

综合图2可知,除ABA外,两地区甜樱桃花芽内其余激素变化趋势相同。单个内源激素的绝对量值代表在某一时期该激素的代谢水平,多个激素之间的相互作用则会影响整个休眠进程。在花芽萌动前,HS花芽内ZRs/GA、ZRs/IAA、ABA/IAA、ABA/GA、IAA/GA的比值分别为0.31、0.41、3.31、2.47、0.75;HB为0.28、0.31、2.72、2.40、0.88;TS为0.31、0.29、1.7、1.8、1.06;HB为0.34、0.25、1.46、1.98、1.35。杭州地区ZRs/GA、IAA/GA的比值较泰安地区低,其余激素比值均较高于泰安地区。

2.3 甜樱桃花芽萌动前其内含物与花器官质量综合分析

2.3.1 甜樱桃花芽形态指标、花器官质量统计 由表1、表2可知,花芽萌动前,单个花芽质量TS>TB>HB>HS,田间观察可见泰安地区的花芽较为饱满。两地区相同品种间,小花数目、子房直径,雄蕊数目差异不显著,泰安地区甜樱桃的雄蕊长度显著大于杭州地区。于盛花期对2个地区2个品种甜樱桃胚囊败育率进行调查,杭州地区胚囊败育率显著高于泰安地区,HS、HB、TS、TB的胚囊败育率分别为75.63%、83.77%、26.67%、28.57%。

2.3.2 甜樱桃花芽萌动前花芽内含物主成分分析 为综合评价在花芽萌动前两地区两品种花芽内营养物质和内源激素水平,将此阶段的9个内含物指标进行主成分分析,提取特征值>1的3个主成分,其特征值分别为6.1117、2.4591、0.4286(表3)。第一、二、三主成分方差贡献率分别为67.91%、27.32%、4.76%,累计方差贡献率达到99.99%,符合分析要求。综合得分F为每个主成分得分与对应贡献率乘积之和:F=F1×67.91%+F2×27.32%+F3×4.76。由表4结果可知,4个编号甜樱桃花芽内含物水平的综合

表1 两地区甜樱桃花芽萌动前花芽指数统计

Table 1 Statistics of flower bud index of sweet cherry before bud initiation in two regions

编号 Region-cultivars	花芽纵径 Flower bud longitudinal diameter/mm	花芽横径 Flower bud diameter/mm	单个花芽质量 Flower bud weight/g
HS	8.27±0.37 c	3.60±0.34 b	0.060±0.000 c
HB	8.43±0.65 bc	4.09±0.41 a	0.065±0.002 bc
TS	8.94±0.52 ab	3.76±0.21 b	0.076±0.005 a
TB	9.20±0.74 a	3.74±0.21 b	0.070±0.003 ab

表2 两地区甜樱花器质量

Table 2 Investigation on flower organ's quality of two region's sweet cherry

编号 Region- cultivars	每个花序花朵数量 Average number of flowers per inflorescence	雌蕊长度 Length of pistil/ mm	子房直径 Diameter of ovary/ mm	雄蕊长度 Length of stamen/ mm	雄蕊数目 Stamens number	胚囊败育率 Embryo sac abortion rate/%
HS	3.93±0.70 a	13.17±1.42 b	1.79±0.29 ab	8.54±0.93 c	33.07±2.58 a	75.63
HB	3.40±0.74 b	13.70±0.81 ab	1.73±0.53 ab	8.72±0.99 c	35.80±5.57 a	83.77
TS	3.93±0.25 a	14.14±0.84 a	1.98±0.17 a	11.83±0.72 a	34.20±3.63 a	26.67
TB	3.27±0.46 b	13.32±0.51 b	1.67±0.15 b	10.07±0.80 b	34.73±3.61 a	28.57

表3 主成分分析方差解释

Table 3 Total variance explained

指标 Index	载荷 Load		
	F1	F2	F3
可溶性蛋白 Soluble protein	0.934 5	0.298 8	0.193 5
可溶性糖 Soluble sugar	0.374 2	0.927 1	-0.021 7
淀粉 Starch	-0.985 5	0.096 7	0.139 2
还原糖 Reducing sugar	0.953 1	0.129 3	0.273 5
游离氨基酸 Free amino acid	0.986 8	-0.161 6	0.011 0
GA ₃	-0.505 9	0.811 2	0.293 2
IAA	0.960 1	-0.213 5	-0.180 4
ABA	-0.968 7	0.189 9	-0.159 8
ZR _s	0.359 4	0.847 6	-0.390 2
特征值 Eigen values	6.111 7	2.459 1	0.428 6
方差贡献率 Proportion of variance/%	67.91	27.32	4.76
累计方差贡献率 Cumulative variance/%	67.91	95.23	99.99

表4 花芽萌动前不同品种花芽内含物的综合得分及排名

Table 4 The comprehensive score and ranking of the contents of flower bud in different varieties before budbreak

编号 Region- cultivars	主成分得分 Principal component score			综合得分(F) Comprehensive score	综合得分排名 Comprehensive score ranking
	F1	F2	F3		
HS	-0.918 6	0.991 7	-0.650 1	-0.384	3
HB	-0.808 0	-1.115 4	0.594 1	-0.825	4
TS	0.784 8	0.680 1	1.082 4	0.770	1
TB	0.941 8	-0.556 5	-1.026 4	0.438	2

得分分别为-0.384(HS)、-0.825(HB)、0.770(TS)、0.438(TB)。因此,在花芽萌动前,甜樱桃此阶段花芽内含物水平TS>TB>HS>HB。

2.3.3 甜樱桃花芽内含物与花芽形态及花器官质量相关性分析 将花芽萌动前9个指标值分别与甜樱桃花芽指数、花器官质量进行相关性分析,得到相关系数矩阵(表5、表6)。结果表明,在本时期内,甜樱桃花芽的可溶性蛋白含量与还原糖含量呈显著正相关,淀粉含量与ABA含量呈显著正相关,与游离氨基酸含量呈显著负相关、与IAA含量呈极显著负相关。游离氨基酸含量与IAA含量呈显著正相关,与

ABA含量呈显著负相关。而此时花芽的纵径与淀粉含量呈极显著负相关,与ABA含量呈显著负相关,与游离氨基酸含量和IAA含量呈极显著正相关,花芽横径与ZR_s含量呈显著负相关,花芽质量与还原糖含量呈显著正相关。雄蕊长度与可溶性蛋白、还原糖含量呈显著正相关,胚囊败育率与可溶性蛋白含量呈显著负相关,与淀粉含量呈显著正相关。由此可见,花芽萌动前其营养物质和内源激素含量与花芽大小及后期花器官发育质量密切相关。

3 讨论

碳水化合物含量的变化为生殖生长提供了一定的营养基础,在花芽形态分化过程中起着重要作用。对橄榄^[3]、苹果^[4]等树种的研究均表明,淀粉在花芽分化时期具有一定作用。蛋白质和氨基酸是植物体内细胞活动、形态构建的重要生理基础,在花芽分化方面同样具有一定作用^[10-12]。对两个杏树品种研究后发现,氨基酸含量与花芽质量具有正相关性,高水平的氨基酸可提高雌蕊的发育质量,降低败育率^[13]。本试验中,泰安地区2个品种甜樱桃在休眠后花芽内淀粉含量逐渐降低,而杭州地区在休眠中大量增加,于花芽萌动前虽少量降低但仍显著高于泰安地区。杭州地区2个甜樱桃品种在进入休眠后花芽内可溶性蛋白含量大量增加,于花芽萌动前降低,而此时泰安地区该指标仍有少量增加,相同品种间比较可知,泰安地区花芽内可溶性蛋白含量显著高于杭州地区。相关性分析表明,甜樱桃胚囊败育率与花芽萌动前氨基酸含量并无显著相关,而与可溶性蛋白与淀粉含量显著相关,花芽内较高水平的可溶性蛋白、较低水平的淀粉,胚囊败育率就相对较低。可溶性糖常被认为是花芽分化重要的营养基础,奈李在花芽生理分化期积累的大量可溶性糖在后期形态分化中被大量消耗^[14]。多数研究表明,较高含量的可溶性糖更有利于花芽分化^[15-17]。本试验

表5 甜樱桃花芽萌动前各项指标与花器官质量相关性分析
Table 5 The correlation analysis of various indexes and flower organ quality of sweet cherry before bud initiation

	可溶性蛋白 Soluble protein	可溶性糖 Soluble sugar	淀粉 Starch	还原糖 Reducing sugar	游离氨基酸 Free amino acid	GA ₃	IAA	ABA	ZR _s	小花数目 Number of flowers per inflorescence	雌蕊长度 Length of pistil	子房直径 Diameter of ovary	雄蕊长度 Length of stamen	雄蕊数目 Stamens number	胚囊败育率 Embryo sac abortion rate	
可溶性蛋白 Soluble protein	1															
可溶性糖 Soluble sugar	0.622	1														
淀粉 Starch	-0.865	-0.282	1													
还原糖 Reducing sugar	0.982 *	0.471	-0.889	1												
游离氨基酸 Free amino acid	0.876	0.219	-0.987 *	0.923	1											
GA ₃	-0.174	0.556	0.618	-0.297	-0.627	1										
IAA	0.799	0.165	-0.992 **	0.838	0.980 *	-0.712	1									
ABA	-0.879	-0.183	0.951 *	-0.942	-0.988 *	0.597	-0.942	1								
ZR _s	0.514	0.929	-0.327	0.346	0.213	0.391	0.235	-0.125	1							
小花数目 Number of flowers per inflorescence	0.167	0.774	0.322	0.036	-0.329	0.942	-0.439	0.300	0.575	1						
雌蕊长度 Length of pistil	0.518	0.107	-0.232	0.602	0.373	0.079	0.185	-0.505	-0.241	0.247	1					
子房直径 Diameter of ovary	0.533	0.674	-0.043	0.483	0.109	0.640	-0.069	-0.194	0.352	0.818	0.742	1				
雄蕊长度 Length of stamen	0.960 *	0.548	-0.748	0.969 *	0.801	-0.084	0.677	-0.847	0.346	0.240	0.736	0.682	1			
雄蕊数目 Stamens number	-0.147	-0.851	-0.117	0.040	0.228	-0.701	0.211	-0.303	-0.900	-0.760	0.348	-0.362	-0.028	1		
胚囊败育率 Embryo sac abortion rate	-0.959 *	-0.512	0.965 *	-0.948	-0.949	0.389	-0.924	0.920	-0.502	0.061	-0.317	-0.275	-0.857	0.086	1	

注: *表示相关性显著($p < 0.05$); **表示相关性极显著($p < 0.01$)。下同。

Notes: *indicates significant correlation($p < 0.05$), ** indicates extremely significant correlation($p < 0.01$). The same below.

表 6 甜樱花芽萌动前各项指标与花芽指数相关性分析

Table 6 The correlation analysis of various indexes and flower bud index of sweet cherry before bud initiation

	可溶性蛋白 Soluble protein	可溶性糖 Soluble sugar	淀粉 Starch	还原糖 Reducing sugar	游离氨基酸 Free amino acid	GA ₃	IAA	ABA	ZR _s	花芽纵径 Flower bud longitudinal diameter	花芽横径 Flower bud diameter	花芽质量 Flower bud weight
可溶性蛋白 Soluble protein	1											
可溶性糖 Soluble sugar	0.622	1										
淀粉 Starch	-0.865	-0.282	1									
还原糖 Reducing sugar	0.982 *	0.471	-0.889	1								
游离氨基酸 Free amino acid	0.876	0.219	-0.987*	0.923	1							
GA ₃	-0.174	0.556	0.618	-0.297	-0.627	1						
IAA	0.799	0.165	-0.992 **	0.838	0.980 *	-0.712	1					
ABA	-0.879	-0.183	0.951 *	-0.942	-0.988 *	0.597	-0.942	1				
ZR _s	0.514	0.929	-0.327	0.346	0.213	0.391	0.235	-0.125	1			
花芽纵径 Flower bud longitudinal diameter	0.837	0.195	-0.995 **	0.879	0.993 **	-0.676	0.996 **	-0.965 *	0.233	1		
花芽横径 Flower bud diameter	-0.369	-0.867	0.223	-0.192	-0.093	-0.404	-0.141	-0.011	-0.985 *	-0.127	1	
花芽质量 Flower bud weight	0.915	0.343	-0.781	0.966 *	0.855	-0.266	0.735	-0.913	0.144	0.789	0.023	1

中,杭州地区甜樱桃在经过休眠期间可溶性糖有所积累,随后逐渐下降,于花芽萌动前,相同品种间比较其含量显著低于泰安地区。相关性分析表明,花芽萌动前可溶性糖含量与花芽大小、质量及最终形成的花器官质量并非显著相关,推测可溶性糖对甜樱桃花器官质量的显著影响并非在花芽萌动前的阶段,可能是伴随花芽萌动后,花器官形成过程中其含量的进一步变化而产生相关影响。结合两地区可溶性糖与还原糖含量的变化可知,两地区花芽内的主要糖组分可能并不相同,杭州地区甜樱桃花芽内大量增加的是非还原糖类,而泰安地区则是以还原糖类为主。田间观察可见在花芽萌动前,泰安地区花芽较为饱满,单个花芽质量较长较重,由相关性分析可知,这与泰安地区甜樱桃花芽内还原糖、可溶性蛋白、游离氨基酸较高,淀粉含量较低密切相关。主成分分析结果也表明,在花芽萌动前杭州地区甜樱桃花芽内含物整体水平低于泰安地区。由此可见,在花芽萌动前杭州地区甜樱桃花芽内贮备供后期花器官分化的营养物质较不充足,尤其是可溶性蛋白、还原糖含量较低,而淀粉含量偏高,这些会对该地区甜樱桃后期花器官发育质量造成一定影响。

营养物质的积累是花芽分化的生理基础,激素调节被认为是成花的关键^[18]。GA常被用作促进种

子萌发的破眠剂,但其对花芽分化起着抑制作用。有研究指出,在花芽分化期外施GA₃会使叶片中可溶性糖和还原糖的含量降低,致使花芽分化进程受到抑制^[19]。ZR可促进苹果树花芽分化,在花芽的生理分化期,受源库关系影响叶芽中细胞分裂素含量极低而花芽中含量却处于高水平^[20]。对暗柳橙摘叶处理会明显减少二氢玉米素含量致使花芽形成数量减少^[21]。花芽形态分化开始后外施BA,可极显著提高花器官发育质量并增加翌年花量^[22]。CTK可部分促进芽的生长,玉米素可对呼吸作用产生刺激从而加强种子的呼吸作用,使人参种子破眠萌发^[23]。IAA对植物成花的作用争议较多,目前认为其对花芽分化并不直接起作用,而是通过与其他激素之间的相互作用对花芽分化产生影响。ABA对花芽分化的作用也较有争议,曾有研究表明在甜橙的现蕾至盛花期间,花瓣与花柱中的ABA含量持续上升,作者认为其含量的增加与受粉后花粉管伸长有关,并就此推测ABA在此阶段含量与花器官形成和开放密切相关^[24]。陈伟等^[25]对兰竹荔枝胚胎发育与内源激素关系的研究表明,相比于正常胚珠,败育胚珠中的ABA含量保持在较高水平,IAA、GA和CTK类激素则较低。在本试验中,于花芽萌动前,杭州地区两品种花芽内ABA含量显著高于泰安地区同一品

种,但此阶段ABA水平与后期胚囊败育率并非显著相关。而花芽分化也并非单一内源激素作用的结果,与多种内源激素相互平衡有关,GA和ABA之间具有拮抗作用,糖类化合物也会在一定的程度上抑制ABA代谢水平。ABA/GA、ABA/ZR、IAA/GA、ABA/(GA+ZR)等比值被认为与休眠的程度密切相关,其中或可能存在一个阈值,当达到阈值,植株进入休眠状态^[26]。而在花芽分化阶段,ZR/GA、ZR/IAA、ABA/IAA、ABA/GA比值的升高被认为可促进花芽分化^[6,19]。段成国对两个品种甜樱桃自然休眠期内内源激素测定的结果表明,花芽中ABA含量呈先上升后下降的趋势,在萌芽前,ABA含量维持在一个较低的水平;GA、ZT含量则在休眠最深时降到最低值,在萌芽前又显著增加;IAA含量波动较大,在休眠解除前大量增加^[27]。本试验中,泰安地区2个甜樱桃品种休眠期内源激素变化与此相同,而杭州地区2个甜樱桃品种在休眠中花芽内ABA含量降到低值,在花芽萌动前升高,ABA含量在萌动前升高并不利于休眠的解除。但综合多种激素的比值分析后可知,除ZR_s/GA的比值略低于泰安地区外,其余激素比值均较高于泰安地区,而较高的比值更有助于打破休眠芽,使其萌发。因此杭州地区2个甜樱桃品种破眠并无异常,但杭州地区IAA/GA的比值较低。该组合比值在苹果上被认为是花芽孕育启动阶段的关键因素,其作用大于ZR/GA₃。花芽萌动前较低的IAA/GA和ZR_s/GA有可能会对杭州地区2个品种甜樱桃花芽萌动后进入花器官进一步发育的起始有所影响。但本试验相关性分析表明,甜樱桃花器官质量与花芽萌动前的GA₃、IAA、ABA、ZR_s含量并无显著相关性,而花芽大小及质量不仅与部分营养物质有关,与内源激素也密切相关,在花芽萌动前,IAA会刺激花芽的纵向生长,而ABA则会抑制花芽纵向生长,ZR_s抑制花芽的横向生长。而在此阶段,IAA、ABA含量又与淀粉和游离氨基酸水平显著相关。

4 结 论

杭州地区甜樱桃花芽内部分营养物质在休眠期内的动态变化规律与泰安地区有所不同,在花芽萌动前内含物整体水平偏低,对该地区花芽指数、雄蕊长度和胚囊败育率等花器官发育质量造成一定影响。植物花器官发育是多种生理因素以及环境等共

同作用的结果,花芽萌动前芽体内营养成分与内源激素含量仅能表明在花器官发育前期的基础。随着花芽萌动后花器官的进一步分化,以及休眠解除后源库关系的影响,营养成分与内源激素含量仍将出现一系列动态变化,尽管尚不知此阶段与花芽发育质量是否存在更显著的相关性,但如何通过栽培措施使树体的养分更有利于提高花芽发育质量亟需进一步研究。

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