

苹果苦痘病发生规律及防治研究进展

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摘要: 钙是苹果生长发育过程中必需的矿质元素之一, 缺钙会导致细胞代谢失调, 引发苹果苦痘病等生理病害, 严重影响果实品质。苹果主要通过根系在土壤中吸收钙, 根系吸收的钙在蒸腾拉力的带动下运往地上部, 而蒸腾作用弱, 导致苹果果实易发生生理缺钙。果实中的钙含量与树种、砧木类型等树体因子和施肥、修剪等农技措施密切相关。综述了苹果苦痘病与钙之间的关系、苹果钙吸收转运、苹果缺钙机制和苹果苦痘病防治的研究进展, 以期为提高果树钙吸收能力, 增加果实钙含量预防苹果苦痘病, 促进果实生长及改善采后贮藏品质, 减轻果农负担, 促进苹果产业健康可持续发展提供理论依据及指导方法。

关键词: 苹果; 钙; 苦痘病; 钙吸收能力; 防治技术

中图分类号: S661.1

文献标志码: A

文章编号: 1009-9980(2024)05-0990-09

Research progress in the occurrence and control of bitter pit disorder in apple

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Abstract: The apple (*Malus pumila*) is a deciduous fruit crop of the Rosaceae family and one of the four most important fruit species in the world. China ranks first in the world in per capita consumption and exports of apples. The apple industry plays a key role in the national economy, but the apple fruit quality in China is poor and the proportion of high quality fruit is low. As we all know, calcium is one of the essential mineral elements in the process of apple growth and development, and it is an important component of the cell wall, which plays an important role in maintaining cell membrane homeostasis and intracellular signal transduction. Too high or low intracellular calcium ion concentrations have a negative effect on apples. Keeping intracellular calcium homeostasis plays an important role in plant growth and development and response to stress. The lack of calcium leads to disturbances in cell metabolism, causing apple bitter pit and other physiological disorders, which seriously affect the fruit quality. Apple bitter pit is a physiological disorder caused by calcium deficiency in fruit, manifested by the rupture of flesh cells and the formation of small, dark-coloured indentations. Apple bitter pit often occurs when fruit is close to ripening and during the time of storage, and is most common in the distal part of the fruit. In apple cell, low concentrations of intracellular calcium reduce the stability of cell walls, cell membranes and membrane-bound proteins, but high concentrations are also toxic to the cell, with high

收稿日期: 2024-01-08 接受日期: 2024-03-11

基金项目: 山东省重点研发计划(2021CXGC010804); 泰安市科技创新发展项目(2021NS089)

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concentrations of calcium ion leading to the formation of phosphate precipitates that interfere with phosphate-based energy metabolism and compete with magnesium ions for enzyme binding sites. Ensuring intracellular calcium homeostasis is important for healthy growth of apple. Calcium homeostasis in the cytoplasm of apple involves a variety of calcium transporters and organelles, which form a complex regulatory network. Apple mainly absorbs calcium from the soil through the root and transports it to the above-ground part under the drive of transpiration pull. Since the transpiration of fruit is low, apple fruit is susceptible to physiological calcium deficiency. At the cellular level, apple mainly absorbs calcium ions through the apoplastic and symplastic pathways in the root vascular bundles, and the above-ground parts of plants can absorb calcium ion through non-vascular bundles. The root system absorbs and transports calcium ion through calcium channels, the superfamily of calcium ion/cation anti-transporters (Ca-CAs) and the P-type Ca^{2+} -ATPase, which transports calcium ion in a chelated state through the xylem to the vigorously growing canopy, including young leaves, flowers, fruits and apical meristematic tissues. In general, apple peel calcium concentration is higher than flesh, and phloem calcium content is higher than xylem. In the early stages of apple fruit growth, calcium is evenly distributed throughout the fruit, but as the season progresses there are differences in concentration, with the highest calcium content in the peel, the lowest in the flesh, and the middle in the seed and centre of the fruit. Fruit calcium content is closely related to tree factors such as cultivar, rootstock type and agronomic practices like fertilization and pruning. The calcium content in fruit trees and the distribution of calcium in the fruit are largely controlled by genes, and different stion combinations also have significant effects on apple fruit calcium content. Calcium uptake by apple is also influenced by the balance of calcium with other mineral elements and total salinity. In addition, overgrowth of fruit trees and competition for calcium between branches and fruit lead to low calcium levels in fruit. External application of various types of calcium fertilizer can increase the calcium content in fruit, improve fruit quality and increase fruit shelf life. Although calcium plays an extremely important role in preventing bitter pit in apples, a single calcium deficiency may not be the key factor in triggering apple bitter pit. Compared to healthy fruit, symptomatic fruit has lower levels of calcium and boron, while the opposite is true for nitrogen, potassium, phosphorus and magnesium; the lower the calcium content in the fruit, the higher the magnesium and potassium content, and the more severe the apple bitter pit disorder. The improvement and enhancement of the fruit quality and appearance will open up more opportunities for our apple industry and will promote its healthy development. This paper reviews the relationship between apple bitter pit disorder and calcium, calcium absorption and transport in apple, the mechanism of calcium deficiency in apple and the progress in research on the control of apple bitter pit disorder, with a view to improving the calcium absorption capacity of fruit trees, increasing the calcium content in fruits to prevent apple bitter disorder, improving the fruit growth and quality during post-harvest storage, reducing the burden of fruit growers, and promoting the development of the apple industry.

Key words: Apple; Calcium; Bitter pit; Calcium absorption capacity; Control technique

蔷薇科落叶果树苹果(*Malus pumila*)是世界四大水果之一,具有较高的营养价值。中国苹果的栽培面积约232.38万 hm^2 、平均年产量4 388.23万t,分别占世界的48%、54%;中国苹果的人均占有率与出口额均位列世界第一;中国现已发展为世界上最大的苹果生产国和消费国^[1-3]。黄土高原、渤海湾、黄河

故道、秦岭北麓和西南冷凉高地是中国苹果的主产区,苹果产业是国民经济的重要组成部分。但中国苹果果实品质较差,优果率低。苹果苦痘病(bitter pit, BP)是影响苹果经济性状的主要病害,尤其在实行套袋栽培后发病日益严重^[4]。

苹果苦痘病是由果实缺钙(Ca)引起的常见的

生理病害,一般在果实接近成熟时开始出现;多发于果顶处,具体表现为果肉细胞破裂,形成小的深色凹陷;降低了果品等级与果实耐储性,严重影响了果实的商品率等经济性状^[4-6]。虽然苹果苦痘病常常发现于果实成熟期和储藏期,但是其发生可能源于果实生长发育的整个时期^[7-8]。有研究指出,品种、砧木类型、树龄、生长势、负载量、营养施肥、果实大小、采收时期和贮藏条件等因素与苹果苦痘病发生密切相关^[9-11]。笔者从苹果钙吸收转运,苹果苦痘病与果树品种、果实生长发育、钙和其他元素的关系,以及预防苦痘病措施等方面,论述了苹果苦痘病发生规律及防治方法的研究进展,并对下一步的研究方向进行了展望。

1 钙与苹果苦痘病的关系

钙不仅参与苹果生长发育和形态建成,更重要的是作为胞外信号和胞内生理生化反应的第二信使调控苹果生长和发育^[12]。钙对苹果品质的影响比氮(N)、磷(P)、钾(K)、镁(Mg)重要,缺Ca会引起苹果果实的生理失调,造成苹果发生苦痘病等病害^[13]。钙具有稳定细胞膜结构、提高苹果抗逆性和减少果实生理病害等多种功能。钙离子(Ca^{2+})/钙调蛋白参与对谷氨酸脱羧酶的激活,而谷氨酸脱羧酶在调控脱落酸(ABA)对苹果苦痘病的调控中起着信号转导的作用^[14]。发生苦痘病的果实中N、P、K和Mg的含量明显高于正常果,而Ca和硼(B)的含量则要低于正常果^[15-17]。Schlegel等^[18]在2002年发现,苦痘病果实与正常果实细胞结构差异主要表现在细胞壁、细胞膜和细胞器3个方面。与健康组织相比,苦痘病组织有更高浓度的草酸和柠檬酸,而过多的草酸和柠檬酸会通过溶解细胞壁的中胶层诱发苦痘病;而钙可以将多余的草酸和柠檬酸转化成不溶性的盐,限制其对细胞壁的破坏^[18]。贮藏过程中果实水溶性钙和果胶钙向磷酸钙及草酸钙的无效化转变,以及由此引起的细胞膜系统结构损伤和功能紊乱,是缺钙导致苹果果实生理失调的重要机制之一^[19]。

大量的研究表明,树木单一的缺钙并不一定会导致苦痘病的发生。苹果苦痘病的发生率与叶和果实中的Ca含量、K/Ca、(K+Mg)/Ca、N/Ca相关,苦痘病果实K/Ca、(K+Mg)/Ca、N/Ca比值高于未发病果实^[20]。在苹果栽培过程中,果实着生位置、土壤类型

和施肥措施等会通过影响果实钙含量进而影响苦痘病的发生^[21]。钙与细胞膜表面的磷脂和蛋白质的羧基相结合,可以提高细胞膜的稳定性和疏水性,增强细胞对钾离子(K^+)、钠离子(Na^+)、镁离子(Mg^{2+})等离子吸收的选择性,从而增强苹果对盐害、冻害、热害、干旱和病虫害等逆境的抗性^[22]。苹果缺钙,在细胞层面表现为:细胞壁解体,细胞壁和中胶层变软;细胞膜结构被破坏,透性增大,细胞内养分外渗,使树体易感染真菌和细菌性病害。外部形态表现为:根系和枝条生长点坏死,幼叶卷曲,叶边缘发黄;果实缺钙时,呈现水浸状,缺钙组织形成凹陷或空腔,果实中多酚氧化物形成的褐色素使缺钙组织呈现出棕褐色^[23]。钙还在调节过氧化物酶(POD)、过氧化氢酶(CAT)和超氧化物歧化酶(SOD)等活性以防止膜脂过氧化过程中扮演着重要角色^[24-25]。用X射线光谱仪分析钙定位与苦痘病发生之间的关系,发现病果果皮组织中的钙含量明显低于健康果实,病斑区果肉中积累大量的钾,在果皮细胞中发生钙外泄,液泡内钙明显减少^[10]。可见,Ca含量、K/Ca、(K+Mg)/Ca、N/Ca与苹果苦痘病的发生率密切相关。

2 钙吸收转运

钙是土壤中存在的最丰富的矿质元素之一,土壤中的钙分为无机态钙和有机态钙两大类,其中大部分的钙以无机态钙的形式存在于土壤固相中,如:硅酸钙、硫酸钙、碳酸钙等是植物不能直接吸收利用的钙^[26]。在自然条件下,植物主要通过侧根发生部位和尚未木栓化的根尖等幼嫩部分从土壤中获取钙,土壤中的钙离子主要通过质流、扩散和根系截获等方式到达植物根系表面,再通过质外体和共质体等途径从表皮细胞转移到皮层,然后转移到中柱,最后随木质部的液流在蒸腾拉力的作用下运输到植物的各个部分^[27]。内皮层中的凯氏带和木栓质是质外体运输的主要屏障。质外体中的 Ca^{2+} 必须通过质膜中的钙离子通道等方式进入内皮层细胞的细胞质^[28-29]。根系对钙的吸收受外界钙浓度影响:外界钙浓度低时,钙的吸收符合米氏酶动力学曲线,是典型的主动运输;外界钙浓度高时,钙的吸收受浓度影响较大,并与蒸腾速率呈线性关系^[30]。

钙在组织中有两种运输途径,一是通过质外体途径(包括细胞壁、细胞间隙及木质部导管等部分)扩散,或通过与细胞壁结合位点结合运输钙,其动力

是扩散和离子交换作用^[31];二是共质体运输,一部分钙以游离态的形式通过钙离子通道、Ca²⁺/阳离子反向转运体(CaCA超家族)和P型Ca²⁺-ATPase等钙转运体吸收和转运钙离子^[32-33]。钙是不易移动的元素,当钙到达这些组织或器官后多数会被固定下来,几乎不再分配。在细胞水平,植物通过钙离子转运系统控制胞质对Ca²⁺的吸收和转运,维持胞质内游离Ca²⁺的静息浓度,既能使胞质中游离Ca²⁺浓度迅速升高以响应环境变化,又能使其维持低浓度状态以防止其对细胞代谢的毒性^[26,34]。

3 苹果缺钙机制

3.1 品种和砧木类型与果实钙含量的关系

果树中的钙含量和钙在果实中的分布很大程度上受遗传调控,不同品种果实成熟时的钙浓度由高到低依次为:新红星>珊夏>粉红女士>千秋>嘎拉>红富士>红将军>新世界^[21]。推测不同品种果实成熟时钙浓度与钙转运蛋白基因表达有关。李宝江等^[35]通过对22个苹果品种的研究发现,不同品种之间的钙含量存在极显著差异,其中钙含量最低的品种(红玉)与最高的品种(富士)相差10.4倍。果梗是连接结果枝与果实的唯一通道,随着果实生长,果梗木质部结构逐渐被薄壁细胞挤压破坏,且果梗维管束的结构和功能逐渐衰退,影响果实钙吸收。斗南苹果果实维管束随着果实生长比富士苹果更早被破坏,功能更早丧失,影响了果实钙积累,导致斗南苹果果实钙含量低于富士苹果^[17]。与富士苹果相比,卡塔琳娜苹果和蜜脆苹果的钙含量低,导致果实易得苦痘病。即使是相同品种,不同的砧穗组合,钙含量的差别也很大:以B9为砧木的富士新梢叶片、短枝叶和果实中的钙含量比以M9、M26、M27为砧木的高^[9]。关军锋等^[36]通过对以山丁子为根砧,以M26、MM106、M9为中间砧的金冠苹果钙含量进行分析,发现在果实采收初期MM106上的苹果果肉钙含量最高。

3.2 树体因子与果实钙含量的关系

与中庸树相比,树体生长过旺,枝条会与果实竞争钙,导致果实中的钙含量降低^[37]。保持果树合理的负载量是控制果实生理病害的一条重要途径:与高负载量树相比,低负载量果树的果实中钙含量较低,包会英等^[38]运用多元分析法研究了秦脆苹果苦痘病的发生规律,发现苦痘病发病率与强营养枝

(0.54)、长秋梢数(0.43)呈极显著正相关,与挂果量(-0.43)呈极显著负相关。

苹果幼树的果实体积偏大,钙含量低,易发生钙稀释现象,果实易发生生理病害^[39-40]。一般情况下,在苹果中,果柄钙浓度高于果肉钙浓度,且韧皮部钙含量高于木质部^[41]。苹果果实生长初期,钙在果实中均匀分布,但随季节推移出现浓度差异,果皮中钙含量最高,果肉最低,种子与果心居中^[42]。

3.3 施肥与果实钙含量的关系

施肥量、肥料元素的配比和施肥时期等施肥技术均与果实钙含量有重要关系。众所周知,肥料的使用提高了苹果的产量和商品率^[43];然而不合理施肥会给苹果生产带来严重后果:施肥量低,不能充分发挥果树的潜力;施肥量过高会导致烧根等现象,影响苹果产量^[44]。氮是蛋白质重要的组成成分,对提高果实品质有重要作用,生产过程中与施用硝态氮相比,施用铵态氮时,富士苹果苦痘病发生率较高^[40];钾是果糖激酶、苹果酸脱氢酶等酶的激活剂,但过量使用钾肥会抑制果树对钙的吸收^[45];镁是三磷酸腺苷(ATP)酶的激活剂,但镁与钙有拮抗作用,大量使用镁肥同样会抑制果树对钙的吸收,具有类似现象的还有锌^[46]。而施硼肥不仅能促进果树对钙的吸收与运输,提高钙含量,而且能减少果实生理病害和贮藏期间的腐烂^[47]。

3.4 果树修剪、果实套袋与果实钙含量的关系

果树修剪可以增强树势,延缓树体衰老,平衡生长势,提升优果率。在冬季对枝条更新修剪可以提高果实、叶片和枝条中的氮、磷、钾、钙含量^[48]。树势过旺会降低花芽形成率、坐果率,导致果实品质下降。夏季修剪能通过去除生长旺盛的枝条,缓解植株郁闭来提高光合效率,合理夏剪还能通过减少枝条生长与果实对有效钙的竞争,促进果实钙积累,降低苹果苦痘病的发生率^[49]。环剥能抑制地上部的光合同化物向地下部转运,促进生殖生长,且有利于花芽形成和提高坐果率,但环剥会抑制地下部生长,阻碍根系对钙等营养元素的吸收,最终导致果实钙含量降低^[50]。苹果套袋可以极大地提高果实的外观品质,降低农药的用量,但会抑制苹果的蒸腾作用,减少果实钙积累^[51]。此外,果实套袋后会影响钙在果实中的分布:套袋果实果皮中钙含量明显低于未套袋果实,而果肉和果心的钙含量却高于未套袋果实^[52]。

4 预防苦痘病的措施

4.1 合理施肥

苹果的产量和品质直接影响果农的收入,而钙作为植物必需的矿质元素在苹果生产中扮演着重要角色,外施不同种类的钙肥均能够提高果实钙含量、改善果实品质^[53]。王树桐等^[54]指出:每生产 1000 kg 苹果,果树需要吸收氮 2.5 kg、磷 0.4 kg、钾 3.2 kg、钙 3.7 kg。果实中 85%的钙来自于土壤,只有 15%的钙从根外追肥中获得^[55]。通过土壤施肥补钙是最为传统的办法,苹果园土壤在春、夏、秋 3 次施肥能显著增加土壤中总钙、交换性钙含量,显著提高成熟果实钙的浓度和钙积累量^[56]。杨兰兰等^[57]通过土施硝酸钙研究长富 2 号最佳的补钙措施,结果表明,在花前、落花后和果实膨大期分 3 次将硝酸钙(0.72 kg·株⁻¹·次⁻¹)施于果树根下的效果最佳。

不利的土壤因素,如土壤盐渍化、土壤温度过低会导致根系活力降低,影响苹果根系的钙吸收^[58]。运输到木质部的钙离子在蒸腾拉力的带动下运往地上部,而植物幼嫩部位及果实的蒸腾速率较低,对钙的竞争小于叶片,加之钙在韧皮部中移动性较差,难以再运输和分配到新生部位及果实,因此果实容易发生缺钙现象^[59]。叶面补钙作为一种快速、高效的补钙措施,对提高苹果品质和产量具有重要作用^[60]。外源喷钙能有效抑制果实变软,维持细胞壁结构的稳定,提高果树的品质和抗逆性^[43,61]。幼果期(落花后 3~4 周)叶面喷钙,苹果树对钙的吸收效率最高^[62];Kalcsits 等^[63]通过 ⁴⁴Ca 示踪试验证实了幼果期蜜脆苹果果实对钙的吸收效率最高,随着果实生长,钙的吸收效率逐渐降低。虽然外施不同种类的钙肥能够提高果实钙含量,但不同钙肥应用效果不同,Ranjbar 等^[53]发现,与氯化钙(CaCl₂)处理相比,纳米碳酸钙(CaCO₃-nano)处理在改善苹果储藏期果实品质方面效果显著;杜英俊^[64]研究表明糖醇钙 800 倍液补钙效果优于氨基酸钙;此外,在果实采收后使用 2%糖醇钙浸泡果实 15 min 能显著提高果实硬度,延长苹果货架期^[65]。在果实发育过程中使用氯化钙、纳米碳酸钙和糖醇钙等钙肥对提高果实中钙含量有积极作用。

近些年,越来越多的研究发现植物生长调节剂会影响果实钙积累。钙作为第二信使,广泛参与生长素(IAA)、赤霉素(GA)和 ABA 信号转导,调节果

实发育和果实软化;而果实发育过程中的激素调节又可以影响钙在果实中的分布^[37,66]。钙主要依靠木质部运输,生长素能改善植物木质部的功能和维管束的数量,增强苹果对钙的运输^[67]。苹果花后喷施 GA₃会促进植物营养生长,导致营养器官与果实竞争钙,增加苹果患 BP 的风险,盛花后喷施 GA 抑制剂,抑制营养生长,则会降低果实中 K、Mg、N 含量,增加果实中 Ca 含量,从而降低发生 BP 的风险^[68]。ABA 可以通过降低植物的蒸腾作用效率和维持木质部功能促进果实的钙积累^[69-70]。因此,在补钙同时添加 IAA、ABA 或 GA 抑制剂等激素会增加果实中钙含量。

4.2 农艺措施

改善园区的栽培条件:通过秋季果园深耕、种植绿肥作物、增施有机肥等途径改善土壤理化性质,能促进团粒结构形成,还能改善根系通风透水性,保证根系正常的呼吸作用,促进根系对钙的吸收^[71]。及时排灌:遇到旱情及时浇水,雨季注意排水,防止树下积水成涝,有利于提高养分有效性,还能保证根系正常生长,提高果实钙含量和品质^[72-73]。合理修剪有利于保持良好的树体结构,改造过密园,减少枝量,能改善树体通风透光条件,同时可缓解生长过盛的营养器官与果实竞争养分,以免导致钙养分浪费^[74]。

5 总结与展望

苹果苦痘病成为中国苹果产业发展的一大限制因素,降低苹果苦痘病的发生率、提高果实品质是果树学研究的一大热点问题。随着科技的发展,基因组学已经成为研究果树钙吸收转运机制的重要手段,而随着钙吸收转运机制的揭示,专家学者可以通过转基因、分子育种等途径促进钙转运蛋白基因表达,增强果树钙吸收,促进钙分配。微生物在土壤养分活化、促进植物生长等方面有重要作用,借助微生物菌或其分泌物来提高苹果钙含量是一项具有应用前景的科学研究课题^[75]。果树中的钙主要依赖根系从土壤中获得,不同的砧穗组合对提升果树钙含量有显著差异^[9]。未来的研究可通过搭配不同的砧穗组合来促进苹果钙吸收,提高钙利用率,降低苹果苦痘病发生率。激素对苹果钙吸收有重要影响,然而植物生长调节剂与钙肥复配对苹果钙积累的研究较少^[67-70]。苹果对不同种类钙肥的吸收利用率不同,可进一步研发苹果吸收利用率高的肥料;套袋可以提

高果实的品质,但果实套袋会通过影响果实蒸腾作用影响果实钙吸收,应进一步研究果实套袋的种类,减少因果实套袋对苹果钙吸收的影响^[76]。笔者在本文中综述了钙与苹果苦痘病的关系、苹果苦痘病发生规律及防治策略的最新进展,为降低苹果苦痘病发生率与提高苹果果实品质提供理论支撑。综合治理、系统防控以获得最优的苹果钙营养,能更好地避免果实生理失调,改善果实采收期的物理性状。

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