

草莓组培快繁脱毒技术研究进展

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摘要: 病毒病是制约草莓产业发展的重要因素之一。本文阐述了4种主要病毒病的危害与传播途径,总结了3种脱毒方式(茎尖培养脱毒、茎尖培养结合热处理脱毒、超低温脱毒)及其原理。围绕草莓组培快繁技术,系统阐述了外植体建立、继代培养、生根培养及驯化等关键环节的技术要点,分析了脱毒不彻底、褐化、玻璃化、污染、变异等问题,对未来建立不同草莓品种成熟高效的组织培养技术进行了展望,旨在为草莓组培快繁及脱毒研究提供参考与帮助。

关键词: 草莓; 组织培养; 草莓病毒

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Research progress on tissue culture, rapid propagation and virus-free technology of strawberry

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Abstract: Strawberry viral diseases have been identified as a major constraint on the growth and sustainability of China's strawberry industry. This article provides a comprehensive overview of four major viral pathogens: Strawberry Crinkle Virus (SCV), Strawberry Mosaic Virus (SMoV), Strawberry Mild Yellow Edge Virus (SMYEV), and Strawberry Vein Banding Virus (SVBV). It details the symptoms associated with each virus, their transmission mechanisms—particularly through aphid vectors and contaminated propagation materials—and the compounded effects of mixed infections on plant health and yield. The synergistic impact of multiple viral infections is noted to significantly reduce productivity and plant vigor, underscoring the importance of effective virus management strategies. To address these challenges, the study summarizes three primary virus elimination techniques: meristematic tissue culture, meristematic tissue culture combined with thermotherapy, and ultra-low temperature treatment (cryotherapy). Each method is explained in terms of its underlying principles and efficacy. Meristematic culture exploits the virus-free nature of apical meristems, as these tiny, actively dividing tissues often remain uninfected due to their rapid cell division outpacing viral replication. Practically, 0.2–0.5 mm apical tips are excised and cultured, yielding virus-free plantlets in 60%–70% of cases for Benihoppe strawberry viruses. Meristematic culture combined with thermotherapy enhances virus inactivation through controlled heat exposure—typically 38–40 °C for 4–6 weeks—weakening viral particles before meristem excision, boosting success rates to 66%–73%. Cryotherapy exploits the difference in frost resistance between viruses and plant meristems, utilizing ultra-low temperatures (–196 °C in liquid nitrogen) to disrupt viral integrity and replication; freezing induces ice crystal formation that ruptures virus-

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containing cells while preserving meristem vitality, achieving 90%+ virus elimination for stubborn pathogens like strawberry mild yellow edge virus. This article conducts a comprehensive and in-depth analysis of the rapid propagation technology in strawberry tissue culture, with a special focus on pinpointing the key factors that have a significant impact on the efficiency and success of the entire process. The physiological state and developmental stage of explants are paramount, as they critically determine the ultimate outcomes of tissue culture. For instance, explants in the vigorous growth phase tend to have higher regeneration potential compared to those in the dormant stage. Hence, it is strongly recommended to select healthy and actively growing plant materials during the appropriate season, such as spring when plants are in a state of robust growth, to maximize survival rates and ensure the successful establishment of cultures. Furthermore, the disinfection duration should be flexibly and appropriately adjusted based on the sampling time and growth condition of the explants. Young and tender explants sampled in the growing season, which are more delicate, require shorter disinfection periods to prevent tissue damage. In contrast, older and tougher explants collected during the dormant period can tolerate a slightly longer disinfection duration to achieve thorough surface sterilization, thereby laying a solid foundation for subsequent tissue culture steps. Additionally, the article investigates the effects of plant growth regulators (PGR) on rooting culture indicators, including root length and rooting percentage. It outlines the essential technical considerations during the pre-transplant hardening and acclimatization phase, aiming to enhance the overall quality of tissue-cultured plants and improve transplant survival rates. Proper acclimatization protocols, including gradual exposure to ambient environmental conditions and appropriate substrate selection, are highlighted as critical steps for ensuring successful establishment of tissue-cultured plantlets in soil. The paper also discusses the optimal medium composition for inducing bud formation in explants, particularly focusing on the selection of plant growth regulator concentrations. It further explores the role of plant growth regulators during the subculture phase, especially their impact on the proliferation coefficient of tissue-cultured plantlets. The study elaborates on how auxins and cytokinins, such as 6-benzylaminopurine (6-BA), indole-3-butyric acid (IBA), and naphthaleneacetic acid (NAA), regulate bud proliferation. It emphasizes that the balance and concentration of these growth regulators are crucial for achieving optimal bud multiplication, and that these parameters should be tailored according to the specific strawberry variety being cultured. For example, in the subculture of Benihoppe strawberry, the optimal combination of plant growth regulatory substances is $1.0 \text{ mg} \cdot \text{L}^{-1}$ 6-BA + $0.2 \text{ mg} \cdot \text{L}^{-1}$ IBA, while the optimal growth regulatory substances in the proliferation medium of Ningyu strawberry is $0.1 \text{ mg} \cdot \text{L}^{-1}$ 6-BA + $0.1 \text{ mg} \cdot \text{L}^{-1}$ NAA. The article also addresses common challenges encountered during tissue culture, including incomplete virus elimination, explant browning due to phenolic oxidation, vitrification (glassy, water-soaked shoots), microbial contamination and mutation. The underlying causes of these problems are analyzed, and potential mitigation strategies are proposed, such as optimizing culture media formulations, adjusting environmental conditions, and employing antioxidants or antimicrobial agents. The study highlights the importance of selecting appropriate gelling agents, regulating light intensity and temperature, and maintaining aseptic conditions throughout the culture process. Finally, the author reflects on the future development of strawberry tissue culture technology, emphasizing the need to develop species- and variety-specific protocols that accommodate the genetic diversity of strawberry cultivars. The ultimate goal is to establish a robust, standardized, and efficient system for propagation and virus elimination, thereby supporting the large-scale production of healthy planting materials. This study aims to provide valuable insights and references for researchers and practitioners in the field of strawberry biotechnology, contributing to the advancement

of sustainable strawberry cultivation practices.

Key words: Strawberry; Tissue culture; Strawberry virus

草莓(*Fragaria × ananassa* Duch.)为蔷薇科(Rosaceae)草莓属(*Fragaria*),营养丰富、经济价值较高,是多年生草本植物,也是世界上分布广泛的浆果类果树。随着市场需求不断增加,草莓的种植面积不断扩大,对草莓苗的需求量也大幅增加。在长期无性繁殖过程中草莓易感染病毒病,导致果实小、品质差、产量低,给农户造成严重的经济损失。传统防治病毒病的方法如使用化学药剂,易造成环境污染与农药残留^[1]。而草莓组织培养是依赖植物细胞全能性,利用草莓茎尖、叶片等外植体快速繁育草莓苗的现代育苗技术,通过组织培养对草莓进行脱毒处理,可降低草莓病毒病发生率并复壮种苗^[2],是实现草莓优质高产的重要手段。

1 草莓病毒病及脱毒方法

1.1 草莓主要病毒病

草莓以无性繁殖为主,该繁殖特性导致植株一旦感染病毒便会传递给后代,且病毒的扩散速度十分迅速。目前,在草莓生长发育过程中比较常见的病毒主要有草莓皱缩病毒(strawberry crinkle virus, SCV)、草莓斑驳病毒(strawberry mottle virus, SMoV)、草莓轻型黄边病毒(strawberry mild yellow edge virus, SMYEV)和草莓镶脉病毒(strawberry vein band virus, SVBV)。通常情况下,若草莓植株仅受单一病毒侵染往往不会呈现出明显的病症,而当受到多种病毒复合侵染时则会表现出显著的发病症状。生产中最常见的是SVBV和SMoV复合侵染,草莓果实减产率为78%~99%^[3]。

1.1.1 SCV SCV于20世纪30年代在美国首次被发现^[4]。SCV的传播方式主要是昆虫传播,感染后新叶会出现不规则黄化斑点或褪绿条纹,叶片边缘卷曲、皱缩,质地变厚且硬脆,且会导致植株矮化,节间缩短。若与SMoV、SMYEV复合侵染时,症状会显著加重,严重时甚至会出现绝收现象。

1.1.2 SMoV SMoV于1937年在英格兰的风梨草莓上被发现^[5]。该病毒引发的典型症状为叶脉失绿、小叶且呈现斑驳状,同时伴随叶柄短缩、叶色不均匀等,是影响草莓生长发育最严重的病毒。

1.1.3 SMYEV SMYEV是20世纪20年代在美国

加州被发现的^[6],是一种较为常见的病毒病,主要通过蚜虫传播。SMYEV单独侵染草莓时,症状不明显,植株会呈现出轻微矮化,生长势稍显衰弱,叶片颜色略淡;而当与SMoV复合侵染时,植株有明显的矮化特征,果实较小且叶片出现褪绿现象。

1.1.4 SVBV SVBV于1952年在Fairfax草莓上被发现^[7]。单独感染后,植株易出现叶片卷曲、叶片黄化等特点,对发育影响不大;但若与其他病毒复合感染,植株发育则会受到显著影响。

1.2 草莓脱毒技术与方法

1.2.1 草莓茎尖培养脱毒 1934年,White^[8]提出的“植物体内病毒梯度分布学说”表明,病毒在植物体内随维管束移动,在茎尖分生组织中因没有维管束系统,病毒只能通过胞间连丝进行传递,速度较慢,因此茎尖生长点病毒的含量较低,是外植体的最佳选择。20世纪80年代,中国开始利用草莓茎尖部位进行组织培养,从此该技术在中国快速发展。

在红颜草莓初代培养中,当茎尖剥取长度为0.2~0.5 mm、0.5~0.8 mm、0.8~1.0 mm时,成活率分别为40.0%、66.7%和86.7%,而脱毒率分别为62.0%、10.2%和0%^[9]。张志宏等^[10]发现,当剥取的茎尖长度为0.2 mm时,成活率为27.5%,SMoV和SMYEV脱除率达100.0%和85.7%;当茎尖长度为0.5 mm时,成苗率为73.3%,而SMoV和SMYEV脱除率分别为73.3%和70.5%,较茎尖长度为0.2 mm时下降近30%。综上所述,在草莓茎尖培养中,茎尖剥取的长度越长成活率越高而脱毒效率越低;反之成活率较低而脱毒效率较高。

1.2.2 热处理结合草莓茎尖培养脱毒 热处理是使病毒蛋白质在高温条件下钝化失活从而达到脱毒的效果。SVBV、SCV等需在较高温度条件或较长热处理培养时间下才能脱除,而在此情况下草莓植株易感染红蜘蛛等病虫害,导致死亡。因此通常使用热处理结合茎尖培养进行病毒的脱除,例如将生长状况较好的草莓苗在38~40 °C下热处理培养4~6周,然后取茎尖进行接种培养^[11]。

1.2.3 超低温脱毒 超低温脱毒是利用病毒与植物分生组织抗冻性的差异,从而实现植株脱毒。植物茎尖分生区细胞含抗冻物质,抗低温能力强,而病毒

无细胞结构,抗冻性较弱。陈曦等^[12]发现,福莓1号草莓在超低温处理后对SMoV病毒脱除率可达100%。黄倩茹^[13]对宁玉草莓进行超低温处理后,SMYEV脱毒率为66.7%,SVBV脱毒率为73.3%。

2 外植体的建立

2.1 取材

2.1.1 外植体选择 草莓组培快繁中外植体选取对后续成败及植株再生质量起到关键作用。目前,已有将茎尖、叶片、花药等作为草莓外植体进行组培快繁的相关研究。1974年,日本首先证明以花药为外植体培养的草莓植株为正常倍性,且可脱除病毒,是培育脱毒苗的手段之一^[14]。茎尖属顶端分生组织,有较强的分生能力,可以高效脱除病毒^[15],是草莓组培中最常用的外植体。由于植物叶片具有再生能力,且取材方便、操作简单,因此可作为高效再生的受体^[16],但由于无法彻底脱除病毒,其应用受到极大限制。

2.1.2 取材时间 草莓匍匐茎最佳取材时间为4—5月,此时气温回升(15~25℃),草莓处于旺盛生长期,匍匐茎萌发数量多、生长速度快,茎段饱满,含有的营养物质(如碳水化合物、生长素)较多、细胞活性较高。其次,9—10月也可取材,秋季气候凉爽(10~20℃),此时植株尚未进入休眠期,匍匐茎仍保持一定的生理活性,且外界病虫害较少,能降低取材后的污染风险。夏季高温多雨时,外植体易携带内生菌,污染风险较高,需谨慎取材。

2.2 初代培养

2.2.1 基本培养基的选择与生长调节剂对不定芽萌发的影响 基本培养基的选择对各类植物组织培养而言是首要前提,它提供组织培养过程中所需的关键营养。在草莓初代培养中,常用基本培养基包括MS和1/2 MS,其中以MS为基本培养基的应用更多。不同基本培养基对外植体的诱导率有所不同。陈甘牛等^[17]研究发现,选用不同基本培养基对愈伤组织的诱导率从高到低依次为MS、1/2 MS、White,在同样添加 $1.5 \text{ mg} \cdot \text{L}^{-1}$ 6-BA+ $0.75 \text{ mg} \cdot \text{L}^{-1}$ IBA的培养基中,诱导率分别为86.67%、40.00%、30.00%。

常用的生长调节剂主要有细胞分裂素和生长素两大类,常用的激素有6-BA(6-苄氨基嘌呤)、IBA(吲哚丁酸)、NAA(萘乙酸)等,不同品种适宜的激素浓度(ρ ,后同)不同。如章姬匍匐茎茎尖在 $1.0 \text{ mg} \cdot \text{L}^{-1}$

IBA+ $0.1 \text{ mg} \cdot \text{L}^{-1}$ IAA的MS培养基上诱导率可达80%^[18],而越秀匍匐茎茎尖在 $1.0 \text{ mg} \cdot \text{L}^{-1}$ 6-BA+ $0.3 \text{ mg} \cdot \text{L}^{-1}$ IBA+ $0.3 \text{ mg} \cdot \text{L}^{-1}$ NAA的MS培养基中诱导率可达100%^[19]。

2.2.2 基本方法 外植体消毒作为组培技术体系的基础环节,其作用在于减少外植体携带的微生物数量,从而为无菌外植体的构建提供保障。植物组织培养中,消毒所用的试剂种类、浓度、处理时间要根据外植体的生长状况及草莓品种而定。目前,草莓外植体消毒常采用的化学试剂有乙醇、升汞、次氯酸钠等^[20-21]。梁峥等^[22]对香野草莓外植体消毒时发现,用5% NaClO处理10 min,流水冲洗后用75%乙醇处理2 min、0.1% HgCl₂处理5~8 min时,茎尖诱导成活率可达87.0%,消毒时间过长会导致外植体褐化率增高,而消毒时间过短则会增加污染率。

草莓茎尖培养时,所剥取的茎尖大小直接影响脱毒率,剥取茎尖越小脱毒率越高,但操作难度更大且成活率越低。生产中一般取茎尖0.5~0.8 mm^[23]。

3 继代培养

3.1 基本方法

草莓继代培养是组培技术体系中的关键步骤,其作用在于保障组培苗实现高效增殖、正常生长与分化,进而为完整植株的形成提供必要条件。选用初代培养获得的健壮无菌苗用于继代培养,通常筛选标准为:株高3~5 cm,带有3~5个发育饱满的侧芽,叶片无黄化、卷曲现象,无叶片透明、质地脆嫩的玻璃化特征,根部无愈伤组织过度增生。在超净工作台内取出无菌苗,置于铺有灭菌滤纸的培养皿中以吸收多余水分,降低污染率。用已消毒的镊子将无菌苗切割为带1~2个侧芽的茎段,长度控制在1~2 cm,去除黄化或破损叶片,转接至培养基中,每瓶接种3~5个茎段,注意避免过密导致营养竞争与通风不良^[24]。

3.2 基本培养基的选择及生长调节剂对草莓增殖的影响

草莓继代培养的基本培养基选择较为单一,大多选用MS培养基。对于添加的生长调节剂来说,常用组合为: $0.5 \sim 2.0 \text{ mg} \cdot \text{L}^{-1}$ 6-BA、 $0.01 \sim 0.1 \text{ mg} \cdot \text{L}^{-1}$ NAA。6-BA作为细胞分裂素主导芽体分化,当其浓度过低时,形成的芽数目减少,但其生长势良好,而浓度过高易导致玻璃化现象产生^[25]。NAA作为生

长素辅助调节,浓度超过 $0.1\text{ mg}\cdot\text{L}^{-1}$ 时易诱导愈伤组织形成,抑制芽增殖^[26]。不同草莓品种在继代培养中对激素种类及浓度的要求也不相同^[27]。甘文娴^[28]发现,在红颜的继代培养中,植物生长调节物质最佳配比是 $1.0\text{ mg}\cdot\text{L}^{-1}$ 6-BA+ $0.2\text{ mg}\cdot\text{L}^{-1}$ IBA。宁玉草莓最优增殖培养基生长调节物质为 $0.1\text{ mg}\cdot\text{L}^{-1}$ 6-BA+ $0.1\text{ mg}\cdot\text{L}^{-1}$ NAA,增殖系数可达9^[29]。

3.3 培养条件

在草莓继代培养时,培养室温度需控制在 $23\sim 26\text{ }^{\circ}\text{C}$,昼夜温差不得超过 $5\text{ }^{\circ}\text{C}$ ^[30]。高温($>28\text{ }^{\circ}\text{C}$)易导致种苗徒长与污染率上升,低温($<20\text{ }^{\circ}\text{C}$)则会抑制芽体增殖速度。采用白色荧光灯提供光照,光照度为 $2000\sim 3000\text{ lx}$,光照时间 $12\sim 16\text{ h}\cdot\text{d}^{-1}$ 。充足的光照可促进种苗的光合作用,避免因光照不足导致的细弱苗现象;光照过强则可能引起叶片灼伤^[31]。培养瓶内相对湿度保持在 $80\%\sim 90\%$,湿度过高($>95\%$)易滋生霉菌,湿度过低($<70\%$)会导致材料失水萎蔫。培养期间每 $3\sim 5\text{ d}$ 观察一次种苗生长状态,及时剔除污染苗与黄化苗,防止污染扩散。草莓继代培养的周期通常为 $30\sim 60\text{ d}$,以红颜草莓为试验材料时发现,继代时间间隔为 40 d 时,植株生长健壮且增殖系数最高,当继代间隔时间为 60 d 时,出现褐化现象^[32]。具体继代间隔时间也因品种特性与培养条件而异。

4 生根培养及驯化

4.1 生根培养

当增殖次数到达一定程度后,就要进入生根培养阶段。草莓生根培养常用的基本培养基为 $1/2\text{ MS}$ 和 MS 培养基,也可选择 $1/4\text{ MS}$ 培养基。有研究表明,当选取 $1/2\text{ MS}$ 作为基本培养基时生根效果最好,生根数可达 13.7 条且生根率达 100% ^[33]。活性炭能够吸附生长过程中产生的一些有害代谢物质。何平等^[34]发现,在添加 $2\text{ g}\cdot\text{L}^{-1}$ 活性炭后,生根数量、生根率、根长等均比不添加活性炭时有所增加。

在生根阶段,常用的生长调节剂有IBA、NAA等,不同草莓品种对植物生长调节剂的种类需求及适宜浓度存在显著差异。柏新富等^[35]发现,添加 $0.05\text{ mg}\cdot\text{L}^{-1}$ NAA对丰香草莓生根有明显的促进作用;王馨等^[36]发现当添加 $0.4\text{ mg}\cdot\text{L}^{-1}$ IBA时,丹莓1号生根表现最优;王禹等^[37]研究发现 $0.5\text{ mg}\cdot\text{L}^{-1}$ IBA+ $0.2\text{ mg}\cdot\text{L}^{-1}$ NAA可促进卡姆罗莎草莓生根。

4.2 炼苗驯化

当生根苗生长 $30\sim 45\text{ d}$ 后、高度超过 3 cm 、根系超过 4 cm 时,需打开瓶盖放置 $3\sim 5\text{ d}$,对组培苗进行瓶内炼苗,以提高瓶苗适应性。炼苗后取出培养基上的生根植株,用自来水冲洗干净后,装入 11 cm 深、 32 孔穴盘中。移栽后的组培苗要置于 $20\%\sim 40\%$ 空气湿度下进行培养^[38]。同时要保证日间温度不超过 $28\text{ }^{\circ}\text{C}$,夜间温度不低于 $21\text{ }^{\circ}\text{C}$ ^[39]。

5 草莓组培中存在的问题

5.1 脱毒不彻底

随着繁殖代数的增加(一般超过 5 代后),病毒逐渐累积,虽然草莓茎尖培养等脱毒体系的不断优化使草莓的种性得以恢复^[40],但由于茎尖剥取难度大、成本较高、诱导成苗时间长等,部分企业难以严格执行标准化脱毒流程,易出现脱毒不彻底、病毒再富集等问题,进而对果实品质与产量产生影响。

5.2 褐化

褐化现象在草莓组培过程中较为常见,其原因是外植体或培养组织中的酚类物质在多酚氧化酶作用下,被氧化形成褐色醌类物质,这些物质积累后会抑制细胞分裂与生长,甚至导致培养材料死亡。植物年龄的增加、光照过强等因素也会增加植物组织或培养基内酚类物质的含量,从而出现褐化现象^[41]。维生素C(Vc)是一种广泛应用于植物组织培养中的抗褐化剂^[42]。付崇毅等^[43]认为,用 $300\text{ mg}\cdot\text{L}^{-1}$ Vc溶液对草莓顶芽浸泡 12 min ,且在培养基中添加 $1.5\text{ g}\cdot\text{L}^{-1}$ 聚乙烯吡咯烷酮(PVP),可在保证茎尖萌发率为 100% 的同时,较好地抑制草莓茎尖褐化。

5.3 玻璃化

组培苗玻璃化是草莓组培过程中常见的问题之一,其本质是细胞过度水化,幼苗出现叶片透明、质地脆嫩等异常现象,从而使组培苗失去活性,影响其正常生长。玻璃化现象与培养环境和生理代谢失衡密切相关,如培养基中蔗糖浓度不当、环境湿度过高或容器透气性较差均可造成此现象的发生。另外,有研究表明,在培养基中添加过高浓度的6-BA也会导致玻璃化现象,当6-BA浓度为 $3\text{ mg}\cdot\text{L}^{-1}$ 时,玻璃化率达 63.64% ^[44]。

5.4 污染

在组织培养过程中,一旦受到细菌、真菌等微生物的侵染,培养物上就会滋生大量菌斑,导致组培材

料无法正常生长和发育。草莓外植体含有大量内生菌,是草莓组培污染的原因之一,这种情况往往出现在6—8月高温的夏季。因此,外植体消毒时间也应根据取材时间灵活选择,尽量避开高温、多雨天气,并适当延长消毒时间。此外,应严格对操作接种环境进行消毒灭菌,降低组培过程中的污染率^[42]。在培养基中添加适当浓度的抗生素也可有效降低污染率^[45]。

5.5 变异

在草莓组培快繁过程中常出现组培苗形态、生理等特性与母株产生明显变异的现象,从而影响组培苗质量。继代次数过多(>10代)、培养基中细胞分裂素浓度过高是变异的重要原因^[46]。有研究表明,当培养基中6-BA添加浓度为 $15\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,草莓组培苗变异发生率显著高于6-BA浓度为 $5\ \mu\text{mol}\cdot\text{L}^{-1}$ 的处理组,变异苗常表现出叶片形态扭曲、匍匐茎分化能力减弱等特征^[47]。

6 展望

草莓是多年生小浆果,营养与经济价值颇高。在消费市场需求持续攀升、设施农业规模化发展的双重驱动下,中国草莓栽培面积呈逐年扩张趋势,产业规模不断壮大。草莓组培快繁技术不仅能为生产提供大量脱毒植株,对草莓种质资源保存也有重大意义。

草莓组培快繁技术具有不受季节限制、繁育速度快、脱毒效率高等优点,在产业化应用中具有重要作用。近年来,草莓组织培养技术取得了显著进展,但从实际需求来看,仍面临诸多亟待攻克的瓶颈问题。主要体现在草莓初代培养过程中的外植体褐化、增殖过程中的玻璃化、病毒脱除不完全、变异等方面。因此建立成熟、高效的草莓脱毒及组织培养技术体系不仅是脱除病毒及草莓快速繁殖的核心解决途径,更是推动草莓产业向高质量、规模化、可持续发展的重要支撑,对提升中国草莓产业的核心竞争力具有重要的现实与长远意义。

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