作物嫁接不親和性

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關鍵字：嫁接、砧木、接穗、嫁接組合、不親和性

摘要：嫁接為古老之無性繁殖方法，可增加作物抵抗環境逆境及病蟲害之能力。嫁接成功與否取決於砧木和接穗之間的親和性，不親和的嫁接組合無法形成健康的植株，容易發生接合處斷裂及提早死亡。嫁接不親和性發生原因包含砧木和接穗之間生理反應不佳、病毒或植原體的傳播及癒傷組織橋中維管束組織異常。研究上可透過嫁接組合之植物荷爾蒙、酚類化合物、葉片氣體交換、礦物質吸收與累積及基因表達等變化，判斷嫁接組合之親和與否。然而植物嫁接不親和性發生原因複雜，誘導發生之機制尚未完全了解，有待後續研究持續探索。

一、前 言

嫁接 (graft)是一種古老的植物無性繁殖法，中國人 (公元前 1560 年)、希臘人和早期基督教已有實行柑橘和橄欖嫁接之紀錄 (Hartmann *et al*., 2011; Melnyk and Meyerowitz, 2015)。嫁接操作方法為將兩個不同個體植物結合，根系 (稱之為砧木)和枝條 (稱之為接穗)兩者之間透過組織再生，結合構成一株新植物(Martínez-Ballesta *et al*., 2010; Cookson *et al*., 2013)。嫁接組合的形成最初需要接合接穗和砧木，並對齊維管束形成層組織，兩者傷口產生反應形成癒傷組織橋，通過癒傷組織橋分化維管束形成層以修復木質部，再由癒傷組織橋的新維管束形成層組織中產生次生木質部和韌皮部(Hartmann *et al*., 2011)。

嫁接可增加植物適應生物性逆境如抗病性 (Ramírez-Gil *et al*., 2017)，以及非生物性逆境之環境條件如乾旱 (Zhou *et al*., 2018)、鹽 度(Mehdi-Tounsi *et al*., 2017)和礦物質缺乏 (Jimenes *et al*., 2018)等。接穗因保有嫁接當下的生長階段，可縮短幼年性時間，使植株有立即生產果實的能力，且矮化性砧木品種可減少種植間距，增加單位面積栽培的數量。該

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技術已廣泛運用於柑橘 (Caballero *et al*., 2013; He *et al*., 2018)、蘋果 (Adams *et al*., 2018; Atkinson *et al*., 2003)、梨 (Hudina *et al*., 2014; Yang *et al*., 2017)、葡萄 (Moreno *et al*., 2014)、李屬 (Zarrouk *et al*., 2010; Pina and Errea, 2008a)和橄欖 (Hussain *et al*., 2016)等作物。

嫁接親和性 (graft compatibility)為砧木和接穗嫁接產生成功的結合，持續發育成一株複合植物，而嫁接不親和性 (graft incompatibility)則為兩者結合失敗。嫁接失敗原因可歸咎於技術不佳、環境條件惡劣、疾病和嫁接不親和性等，而發生嫁接不親和性原因包含砧木和接穗之間生理反應不佳、病毒或植原體的傳播及癒傷組織橋中維管束組織異常。

然而嫁接親和性與不親和性之間的區別並不是十分明確且難以預測，嫁接組合兩者在分類學上親緣越近，嫁接成功的機率越大 (Andrews and Maruez, 1993)，同一科不同屬的嫁接組合親和性低，但同一屬內不同種的嫁接組合可形成有效的結合而存活 (Goldschmidt, 2014)。嫁接操作產生的傷口破壞了植物的維管束系統 (Asahina and Satoh，2015)，因此必須重新連接以維持正常的水分和養分運輸，多數單子葉植物沒有維管形成層，可能是嫁接失敗的原因(Sachs, 1981; Melnyk and Meyerowitz，2015)，這也顯示傷口癒合過程中的維管束分化是嫁接成功的先決條件，但不同的分類群嫁接組合上成功的需求條件可能有所不同 (Rom and Carlson, 1987)。

二、嫁接組合的形成

癒傷組織細胞來自於接穗和砧木，嫁接初期透過快速分裂的癒傷組織細胞分化形成維管束形成層和相關的維管束系統。嫁接親和性的發育包括三個主要過程:1.砧木和接穗的粘附、2.癒傷組織細胞在嫁接接合處或癒傷組織橋增殖、3.嫁接交界處的維管束分化。因此砧木和接穗接合處形成癒傷組織是嫁接的第一反應，嫁接失敗則歸咎於接合處缺乏癒傷組織的形成。

後續的研究進一步提出 (Yin *et al*., 2012)，嫁接最初由傷口刺激未受損細胞消除切口表面細胞碎片，清除細胞碎片過程中，嫁接接合處的接穗和砧木之間細胞緊密接合而產生信號的交換，因而重建接合處的通信網絡，一旦通信重建，生長素即開始積累，特別是對維管束的重新連接產生作用的生長素，最後細胞在生長素的控制下分化為維管束組織，使得接穗和砧木之間的維管束系統重新連接，完成嫁接修復過程中的關鍵步驟，維管束系統重新連接也表示嫁接的成功。mRNA 信號在嫁接後 24 小時發生變化，48 小時後生長素增加並刺激細胞分裂和分化，第三天物質已經在嫁接組合中運送 (Koepke and Dhingra, 2013)。

三、嫁接不親和性類型

嫁接親和性被認為是一種識別系統，由質膜釋放的分子結合形成具有催化活性複合物，

隨後啟動發育程序，最後發展成為一個成功的嫁接組合。為了保持植株功能運作正常，嫁接時砧木與接穗必須緊密，為礦物質、水、同化物和荷爾蒙吸收及轉移提供具有運行功能的系統 (Martínez-Ballesta *et al*., 2010; Gregory *et al*., 2013; Koepke and Dhingra, 2013)。相反的，嫁接不親和性的植株無法形成強壯且持久的功能性結合，容易發生接合處斷裂及植株提早死亡 (Zarrouk *et al*., 2006)。在李屬物種中櫻桃及杏常發生，尤其是杏的不親和性造成栽培上的一個問題 (Lang and Ophardt, 2000)。

嫁接不親和性分為易位嫁接不親和性 (translocated graft incompatibility)和局部嫁接不親和性 (localized graft incompatibility)兩種，易位嫁接不親和性常發生於嫁接後第一年，表現特徵為嫁接組合生長停止、葉片掉落和變色等 (Herrero, 1951; Reig *et al*., 2018)，常發生在桃和李的嫁接組合，這種形式的不親和性與嫁接組合接合處的生化和功能改變有關，由於韌皮部碳水化合物的運輸逐漸受到損害，使得澱粉在嫁接處上方積累而產生毒害 (Breen and Muraoka, 1975; Moing *et al*., 1990)。澱粉逐漸積累會嚴重干擾營養物質代謝和引起根飢餓症狀 (Moing and Gaudillere,1992)，這種現象類似因環剝所產生的破壞 (Li *et al*., 2003; Goren *et al*., 2004)。

局部嫁接不親和性表現較輕微且會延遲發生，表現特徵為接合處之維管束和形成層斷裂而不連續，連接不良亦導致嫁接組合的機械性衰弱 (Errea *et al*., 2001; Zarrouk *et al*., 2010; Hartmann *et al*., 2011; Koepke and Dhingra, 2013)，這類型的不親和性植株在嫁接多年之後或是外力破壞而顯現，對果園經營上產生重大的經濟損失。

四、影響嫁接親和性之因子

（一） 植物荷爾蒙 (phytohormones)

植物荷爾蒙涉及植物的發育，因此被認定其參與調節砧木和接穗之間的生理作用 (Sorce *et al*., 2002; Aloni *et al*., 2010; Koepke and Dhingra, 2013)，其中生長素 (Auxin, AX)和細胞分裂素 (Cytokinin, CK)對於嫁接植物維管束組織形成具有重要的作用 (Melnyk *et al*., 2015)，也是影響細胞生長和組織分化的信號分子 (Aloni *et al*., 2010)。細胞分裂素在根部產生並向上運移至接穗，在接穗上控制重要的植物生育，例如枝條生長(Elfving and Visser, 2006)，而生長素會影響細胞分裂素生成和活性，枝條中的生長素生成與根部中的細胞分裂素生成之間存在強烈的相互作用，具有調節根與枝條生長的功能 (Bishopp *et al*., 2011)。

（二） 酚類化合物 (phenolic compounds)

酚類化合物為存在於高等植物中的次級代謝物，其參與植物體內代謝作用，當植物體受到環境逆境及病原體侵襲等刺激時產生反應 (Errea, 1998; Leonardi and Romano, 2004; Cohen *et al*., 2007; Pina *et al*., 2012)。酚類化合物對於接穗與砧木組合之間的早期結合生長

階段很重要 (Liu, 2012; Herrero *et al*., 2014)，因木質部組織的細胞壁是由酚類化合物 (例如木質素)、多醣、礦物質和蛋白質組成的動態結構。反式肉桂酸是一種經由苯丙胺酸裂解酶作用，衍生自苯丙氨酸的代謝產物，調控類黃酮化合物的合成及木糖生成和木質素的形成，並被視為是環境逆境的標誌物 (Rogers and Campbell, 2004)。此外，酚類化合物的存在已被認為是評估接穗和砧木之間嫁接親和性的重要指標物質 (Prabpreea *et al*., 2018)。

杏與李嫁接組合中，嫁接不親和性的接穗和砧木接合處含有高濃度的酚類化合物 (Errea *et al*., 2001; Pina *et al*., 2012)，酚類化合物的積累會減少生長素含量，影響木質部和韌皮部分化與木質化 (Errea, 1998; Liu, 2012)，也導致生長素降解，進而破壞細胞功能和影響生化反應 (Hartmann *et al*., 2011)。Pina和Errea (2008 b)證明嫁接不親和性的李屬植物中，苯丙胺酸裂解酶轉錄增強，使得苯酚 (如花青素、黃烷酮、對香豆酸和羥基苯甲酸)在植體中積累，導致杏 (Errea *et al*., 2001)和桃嫁接後親和性下降 (Zarrouk *et al*., 2010)。

（三） 葉片氣體交換

嫁接植物的葉片氣體交換直接受到砧木的影響 (Xu *et al*., 2015; Baron *et al*., 2017)，藉由嫁接方式改變接穗的活力和生產力，可透過接穗葉片中葉綠素含量 (Rouphael *et al*., 2008)和光系統 II (PSII)的效率 (He *et al*., 2009)證明。當在接穗與砧木接合處形成癒傷組織橋時，嫁接植物可使水從砧木流到接穗，當不足時會致使水流量減少，從而導致碳同化和氣孔導度的損失 (Magalhães-Filho *et al*., 2008)。

（四） 礦物質吸收及累績

土壤中養分的吸收受到多種因素的影響，包括土壤性質 (酸鹼值、陽離子交換能力和養分濃度)和根系特徵(根系結構、有機酸、代謝產物的滲出能力以及運輸能力)。接穗和砧木會影響根系和葉片中離子積累，進而改變植物的生長和發育 (He *et al*., 2009; Nawaz *et al*., 2016)，因為旺盛的砧木根系具有高含量的糖、氨基酸和酶，亦會分泌有機酸，可吸收大量養分並將其運輸至接穗，因此砧木會影響養分的吸收和利用 (Jaitz *et al*., 2011；Khorassani *et al*., 2011；Dam and Bouwmeester, 2016)。砧木攝取礦物質元素能力會影響枝條生長，從而控制嫁接組合對養分的需求 (Savvas *et al*., 2010; Marschner, 2012)，可藉由測定葉片中養分含量，研究嫁接組合之親和性 (Rouphael *et al*., 2008)。

（五） 基因表達

RNA 為遺傳信息的重要載體，植物體內之病毒 RNA 基因組、內源性細胞 mRNA 及小的非編碼 RNA 可經由胞間連絲進行長距離運輸(Kehr and Buhtz, 2008)，其中 mRNA 和小 RNA (miRNA 和 siRNA)透過非細胞自主途徑機制，以 RNA-蛋白複合物 (如 GAI、CmGAIP、PEP-Let6、BEL-5 及 CmPP16)在砧木和接穗之間運輸 (Zhang *et al*., 2012)。

Xu 等人 (2010) 測定蘋果內源性 GAI mRNA 的運輸，嫁接後第 5 天起在嫁接組合中可檢測到接穗和砧木的 GAI mRNA，顯示 GAI mRNA 透過兩者的結合而向上和向下移動。

Kanehira 等人 (2010)利用激光捕獲顯微切割術，分析蘋果嫁接組織之韌皮部細胞衍生的 cDNA，檢測到多種 mRNA，並對其中之一 MpSLR / IAA14 進行研究，結果表明韌皮部 RNA 轉運系統可能參與砧木對接穗生長之影響。

五、結語

影響嫁接組合產生之嫁接不親和性的因子包含植物荷爾蒙、酚類化合物、葉片氣體交換、礦物質吸收與累積及基因表達等，可利用植物分類學及嫁接後維管束形成之良窳，早期判斷嫁接組合之親和能力，後續藉由代謝作用之光合作用、植物荷爾蒙及酚類化合物含量等變化，作為辨識嫁接不親和性之依據。基因分子鑑定技術的建立，將有助於研究人員對嫁接不親和性的了解，並提供砧木選擇或育種時，一個可行且有效的檢測工具。植物嫁接不親和性發生原因複雜，誘導發生之機制尚未完全了解，有待後續研究持續探索。

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Graft Incompatibility of Crops

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Key words：Grafting, Rootstock, Scion, Graft union, Incompatibility

Grafting is a method for asexual reproduction, and it can help increase the ability of crops to resist environmental adversities and pests. The success of grafting depends on the compatibility between rootstock and scion, for incompatible grafting combination cannot produce strong plants, which are prone to break at joints and early death. As for the causes of graft incompatibility, they include poor physiological response between rootstock and scion, transmission of virus or phytoplasma, and abnormal vascular tissue at callus bridge. In research, the compatibility of grafting combination can be determined through changes in plant hormones, phenolic compounds, leaf gas exchange, mineral absorption and accumulation, and gene expression. However, the causes of graft incompatibility for plants are rather complex, and the mechanism of induction occurrence is not yet fully appreciated, so that it requires further research for continuous exploration.

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