

植物病原卵菌之抗藥性

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摘 要

本文乃針對近十年來在卵菌抗藥性研究之進展做一概述，並對卵菌抗藥性族群之防治，提出管理看法，以為將來田間防治時之參考。卵菌綱類殺菌劑可分成 r-RNA 聚合酶抑制劑(Polymerase inhibitor)、苯醌外部抑制劑(Quinone outside inhibitor, QoI)、羧酸醯胺類(Carboxylic acid amides)、氰基乙酰胺肟類(Cyanoacetamide-oxime)等選擇性殺菌劑，以及銅劑、鋅錳乃浦、四氯異苯睛等多作用點殺菌劑。近年來在卵菌抗藥性的研究，主要集中在抗藥基因及田間抗藥族群的監測。於抗藥基因研究中，晚疫病菌容易對右滅達樂等 r-RNA 聚合酶抑制劑類藥劑產生抗藥性，屬高風險抗藥性高的殺菌劑，在抗藥管理上，深受世界各國重視。QoI 類屬於呼吸作用抑制劑，抗藥性主要是由細胞色素 b 基因上的 G143A 點突變所造成，葡萄露菌容易對 QoI 產生抗藥性族群，但是在停止施用 QoI 後，抗藥性族群有下降趨勢，屬中度抗藥性風險藥劑。羧酸醯胺類則由 2 個隱性基因調控，屬低到中度抗藥性風險的殺菌劑，真正的機制目前不明。歐盟對田間抗藥性族群的管理，主要是由殺菌劑抗藥性行動委員會(Fungicide Resistance Action Committee)工作小組執行，依據每年抗藥性監測結果提出抗藥性管理策略，供歐盟各國參考應用。國內作物及病害屬複雜且多變的類型，如何建立田間抗藥性族群之長期偵測及監測計畫，依據計畫結果做為田間抗藥性管理的依據，應是目前主管單位應強化之施政重點之一。

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關鍵詞：卵菌、疫病菌、露菌、抗藥性

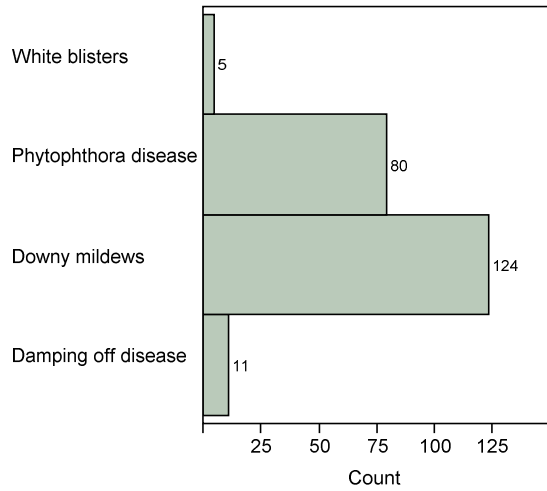
卵菌分類及其重要植物病原菌種類

卵菌原本列於真菌門下，然目前依據化石與分子生物之物種演化分析結果，有學者建議將卵菌綱移至纖毛菌界(Stramenopila)(Barr, 1992)，無論其演化分類，就其為害植物之卵菌種類，主要有露菌(downy mildews)、疫病菌(*Phytophthora* spp.)、猝倒病菌(*Pythium* spp.)及白銹病菌(*Albugo* spp.)等 4 大類，其中又以露菌及疫病菌最受重視，因其為害範圍為主要之經濟作物，包括葡萄、十字花科蔬菜、葫蘆科蔬菜、萵苣，以及果樹、園藝等作物(Hsu *et al.*, 2002)。

抗卵菌綱之殺菌劑種類及其作用機制

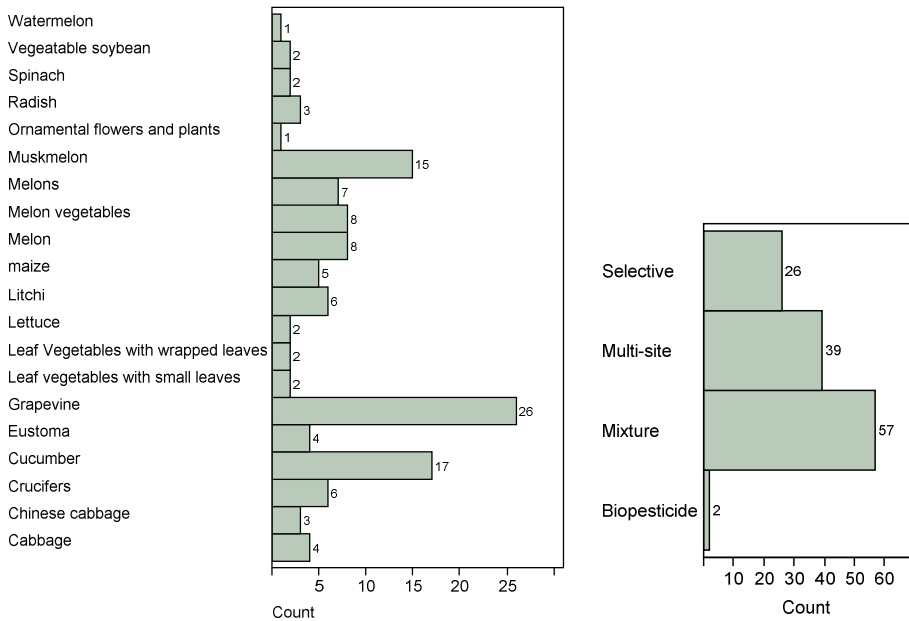
由於卵菌綱為害的作物種類，大都為重要經濟作物，因此許多殺菌劑研發與登記申請，其登記之害物對象大多集中在卵菌綱內的露菌及疫病菌，2006 年全球用於防治卵菌綱的市場約 12 億美金，而以防治露菌病佔有抗卵菌綱殺菌劑最大的市場比例，就防治露菌病的市場裡，防治葡萄露菌病者佔 54%，胡瓜露菌病佔 12%，萵苣露菌病佔 8%等，而登記防治馬鈴薯及番茄晚疫病比例，約等同於葡萄露菌病所佔的額度，明顯地呈現主要作物上主要害物的用藥需求及市場特徵(Gisi and Sierotzki, 2008)。分析國內殺菌劑登記情形，其登記於疫病、露菌病及其他卵菌綱之藥劑種類情形，也呈現類似現象，目前分別有 124、80、11 及 5 種等不同劑型之殺菌劑分別登記於防治國內作物之露菌病、疫病、猝倒病及白銹病(圖一)，總計 223 種。在防治露菌病方面，分別有 26、17 及 15 種等不同劑型之殺菌劑登記在防治葡萄、胡瓜及洋香瓜等作物露菌病(圖二、左)，而防治疫病方面，也有 17 及 11 種等不同劑型之殺菌劑登記在防治番茄及馬鈴薯疫病及晚疫病(圖三、左)。

由上述國內登記情形，清楚地呈現出在農民需求與廠商基於市場考量下的登記現況，分析藥劑種類之登記情形，於防治露菌病方面，則是以混合劑的比例最高，多作用點者次之，分別為 46.0% (57/124)及 31.4%



圖一、登記於防治疫病、露菌等卵菌綱病害的殺菌劑數量。

Fig. 1. The distribution of registered fungicides which control plant diseases caused by Oomycetes, including *Phytophthora*, downy mildews etc.

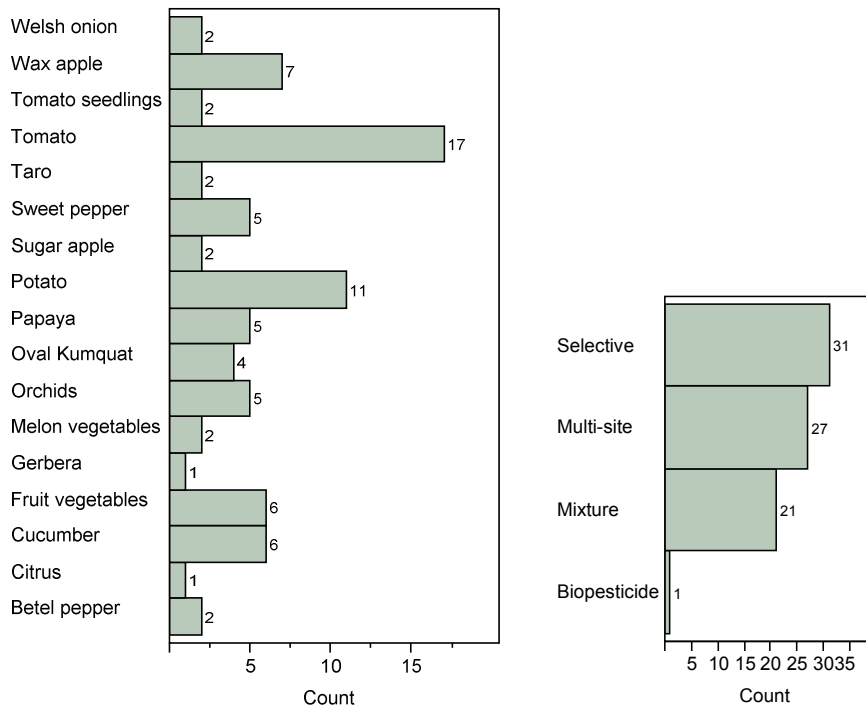


圖二、不同作物露菌病之登記數量(左)及其藥劑類型種類(右)。

Fig. 2. The distributions of fungicides registered to control downy mildews on different crops (left) and fungicidal classifications (right).

(39/124) (圖二、右)，防治疫病方面，選擇性殺菌劑佔的比例最高，多作用點者次之，分別為 38.7% (31/80)及 33.7 % (27/80) (圖三、右)，若登記的藥劑在無管理規劃下，長期使用同類型殺菌劑，容易導致藥效喪失之抗藥性情形，為避免田間抗藥性害物產生之速度與機率，對於抗藥性管理需加以規劃及因應，故於了解抗藥性產生之內在及外在原因之前，應首先了解有那些殺菌劑可應用於防治卵菌綱類之植物病原菌，其作用機制為何，如此方可規劃適當之抗藥性管理策略，底下就抗卵菌綱類殺菌劑種類及其作用機制(Brent and Hollomon, 2007; Lee, 2008)做一簡介：

一、保護劑或多作用點殺菌劑：銅劑、二硫代氨基甲酸鹽類及衍生物 (Dithiocarbamates and relatives)、鄰苯二甲醯亞胺類(Phthalimides)、



圖三、不同作物疫病之登記數量(左)及其藥劑類型種類(右)。

Fig. 3. The distributions of fungicides registered to control *Phytophthora* diseases on different crops (left) and fungicidal classifications (right).

氯化腈類(Chloronitriles)，此類殺菌因抑制真菌之效果屬多作用點，因此不易產生抗藥性問題，其藥劑種類及作用機制如表一。

二、治療劑或選擇性殺菌劑：此類藥劑作用點單一，具治療效果，由於作用點單一，因此容易產生抗藥性問題，其作用機制分類及藥劑種類如表二。

表一、抗卵菌綱殺菌劑之多作用點殺菌劑種類及其作用機制

Table 1. Multi-site fungicides and their mode of action against Oomycete

FRAC code ¹⁾	Group name	Common name	Mode of action
M1	Inorganic	Bordeaux mixture, cupric hydroxide, copper oxychloride, cuprous oxide, copper sulfate, oxine-copper etc.	Enzymes and proteins are denatured after cupric ions binding thiol group on the enzyme or proteins.
M3	Dithiocarbamates and relatives	Ferbam, mancozeb, maneb, metiram, propineb (restricted use in Taiwan), thiram.	Binding the thiol group on amino acids, proteins and enzymes. Sulfur blocked the electron receptor of cytochrome C on mitochondrial electron chain and interfered the mitochondrial respiration.
M4	Phthalimides	Captan etc.	Interfering the mitosis procedure and causing the death of fungal cells.
M5	Chloronitriles (phthalonitriles)	Chlorothalonil	Deactivating the thiol group in fungal cells and interfering the glycolysis and energy production.

¹⁾ FRAC code, code used by Fungicide Resistance Action Committee. Numbers and letters are used to distinguish the fungicides groups according to their cross resistance behavior. M, multi-site inhibitors.

表二、抗卵菌綱殺菌劑之選擇性殺菌劑種類及其作用機制

Table 2. Selective fungicides and their mode of action against Oomycetes

FRAC code ¹⁾	Group name	Common name	Mode of action
A1.	Phenylamides	Benalaxyl, benalaxyl- <i>M</i> (Kiralaxyl), metalaxyl, metalaxyl- <i>M</i> (mefenoxam), oxadixyl etc.	Blocking the ribosomal RNA polymerase I, resulting in the inhibition of the ribosomal RNA synthesis.
B3.	Benzamides	Zoxamide	Binding the β -subunit of tubuline, disrupting the microtubule cytoskeleton, then preventing the nuclear division.
B5.	Delocalization of spectrin-like protein	Fluopicolide	Causing the redistribution of spectrin-like proteins from the membrane to cytoplasm. These proteins maintain the stability in Oomycetes and Ascomycetes.
C3.	QoI -fungicides (Quinone outside Inhibitors)	Azoxystrobin, pyraclostrobin, trifloxystrobin, famoxadone etc.	Blocking the electron transfer between cytochrome b and cytochrome c1 at the ubiquinol oxidizing site and resulting in the inhibition of mitochondrial respiration.
C4.	QiI -fungicides (Quinone inside Inhibitors)	Cyazofamid, amisulbrom	Inhibiting the ubiquinone reducing site (Qi) of cytochrome bc1, then blocking the mitochondrial respiratory chain.
F3.	Heteroaromatics	etridiazole	Blocking the mitochondrial respiratory chain by peroxidizing the membrane lipid.
F4.	Carbamates	Propamocarb hydrochloride	Inhibiting the phospholipid and fatty acid biosynthesis, then the cell membrane permeability affected.
H5.	CAA -fungicides (Carboxylic Acid Amides)	Dimethomorph, mandipropamid	Inhibiting the phospholipid biosynthesis and cell wall synthesis.
27	Cyanoacetamide-oxime	Cymoxanil	Mode of action is unknown. Contact and local systemic activity with protective and curative action, and also inhibits sporulation.
33	Phosphonates	Fosetyl-Al	Mode of action is unknown. Inhibiting the germination of spores or blocking the development of mycelium and sporulation. Systemic activity with acropetal and basipetal translocation.

¹⁾ FRAC code, code used by Fungicide Resistance Action Committee. Numbers and letters are used to distinguish the fungicides groups according to their cross resistance behavior.

抗藥性研究之進展

苯醯胺類(Phenylamides)

本類型殺菌劑包括右滅達樂(mefenoxam, metalaxyl-M)、本達樂(benalaxyl)等抗卵菌綱殺菌劑，其作用機制已被證實是抑制核醣核酸聚合酶複合體 I，進而達到保護及治療效果，但是該類藥劑所作用的基因與序列現在仍不清楚(Davidse, 1995)。這類型藥劑已於田間使用超過 28 年以上，往往在施用後，田間快速產生抗藥性族群，已知有葡萄露菌病(Staub and Sozzi, 1981)、胡瓜露菌病(Reuveni *et al.*, 1980)、萵苣露菌病(Crute, 1987)及馬鈴薯晚疫病(Davidse *et al.*, 1981)。

這類殺菌劑雖然在田間產生抗藥性的速度很快，但是田間抗藥性族群也常隨年份或甚至季節而有所變化(Gisi, 2002; Gisi *et al.*, 2007)，其中又涉及調查地區施藥種類的影響，馬鈴薯晚疫病病菌也有類似現象(Gisi and Cohen, 1996)。抗右滅達樂之晚疫病病菌的基因屬半顯性基因(Knapova *et al.*, 2002)，在葡萄露菌抗右滅達樂的基因則與疫病病菌不同，可能與露菌在遺傳交換及其他生物特性有關(Gisi *et al.*, 2007)。

苯醯外部抑制劑(QoI fungicides)

本類型殺菌之作用機制主要在結合苯醯外部位置，抑制細胞色素 b (Complex III) 的電子傳遞，進而抑制真菌粒線體的呼吸作用，作用位置為真菌蛋白質環形成 glutamic acid 的第 272 位置(Gisi, 2002)。自從發現小麥白粉病菌抗 QoI 殺菌劑的突變基因，即當病原菌細胞色素 b 基因在 143 的 glycine 突變成 alanine 後，就具抗 QoI 類殺菌劑的效果(Sierotzki *et al.*, 2000)，隨後 G143A 抗藥基因在其他真菌中被陸續發現，包括葡萄露菌(Heaney *et al.*, 2000)、胡瓜露菌(Heaney *et al.*, 2000; Ishii *et al.*, 2001) 等。第二個突變點為 F129L，即 129 位置的 phenylalanine 突變為 leucine，這在少數的葡萄露菌(Sierotzki *et al.*, 2005)及猝倒病菌(*Pythium aphanidermatum*) (Gisi *et al.*, 2002)可發現此一抗藥基因，但是在晚疫病病菌、萵苣露菌、*Peronospora* spp.及所有銹菌則未發現 QoI 抗藥族群，原因可能在於 G143A 的突變對這些病原菌是致死突變，因此無法在田間產生抗 QoI 族群(Gisi and Sierotzki, 2008; Grasso *et al.*, 2006)。抗 QoI 的葡

萄露菌首先於 2000 年偵測到，之後全歐到處可見此一抗藥族群，在巴西曾就此進行一個試驗，發現停用 QoI 三年後，抗 QoI 族群有下降趨勢，一旦施用 QoI 後，抗 QoI 族群又快速上升(Sierotzki *et al.*, 2008)。對於為何 G143A 抗藥族群在田間快速產生的原因，目前僅知由於葡萄露菌的基因多樣性變化快(Scherer and Gisi, 2006)、有性世代短、菌系遷移性低的生物特性下，在有 QoI 殺菌劑施用情形下，使得葡萄露菌快速產生 G143A 抗藥族群，一旦停用 QoI 殺菌劑，因上述葡萄露菌的生物特性，又快速地恢復成不具抗藥性的族群，因此 QoI 殺菌劑為中度抗藥性風險藥劑，在管理上須搭配其他不同作用機制的抗卵菌綱殺菌劑使用，即可降低或延緩此類抗藥性族群產生的機會或蔓延的速度。

肉桂酸醯胺類(Carboxylic Acid Amides, CAA fungicides)

本類型藥劑包括達滅芬及曼普胺等抗卵菌綱類殺菌劑，其作用機制目前僅知干擾細胞壁結構及組成，進而造成卵菌無法發芽(Jende *et al.*, 2002)，雖然世界各國田間已有葡萄露菌的抗藥性報告(Gisi *et al.*, 2007)，但是產生抗藥性的基因突變點仍不清楚，藉由抗感性配對之子代抗感性比的結果，抗 CAA 殺菌劑的基因應該是 2 個隱性基因在調控(Gisi *et al.*, 2007)，又經由田間試驗證實，曼普胺停用 2 年後，抗藥性族群呈現明顯的下降趨勢，若在低抗藥性族群區域，連續單獨施用 6 次 CAA 殺菌劑，田間抗藥性族群比例迅速增加，這些試驗結果指出抗 CAA 族群對環境的適應力低於敏感性族群，由此可知葡萄露菌抗 CAA 的風險應為中度風險。另外歐盟雖對晚疫病菌抗 CAA 殺菌劑進行長期監測，但是到目前為止，尚未在田間偵測到抗 CAA 菌株(Cohen *et al.*, 2007)，僅於室內產生不穩定的抗藥性族群(Rubin *et al.*, 2008)。猝倒病菌對 CAA 殺菌劑本身就不敏感，因此無抗藥性問題。

其他抗卵菌綱類殺菌劑

克絕的作用機制並不清楚，因為它的持久性不佳，常和多作用點類殺菌劑製成混合劑，目前僅知義大利及法國的部分葡萄園有有抗克絕的葡萄露菌族群(Genet and Vincent, 1999)，在晚疫病菌方面，則無抗克絕的報告。扶吉胺可阻止卵菌 ATP 產生而達到抑制作用(Gisi, 2002)，目前

無抗藥性族群記錄。普拔克可干擾細胞膜通透性，但真正的作用機制目前則不清楚，卵菌綱中僅猝倒病菌有抗藥性報告(Moorman and Kim, 2004)。福賽得及其分解的亞磷酸可被植物快速吸收及轉移，具有刺激植物產生抗性反應的間接效果，以及改變磷酸化醣含量與細胞壁組成的直接效果(Gisi, 2002)，但是福賽得的作用機制目前也是不清楚，田間也未發現抗福賽得的卵菌類族群。

在抗卵菌綱殺菌劑種類中，有一大半是多作用點殺菌劑，如銅劑、鋅錳乃浦、四氯異苯腈等，因其非系統性、預防性的特性，常被用做保護性殺菌劑，這些藥劑佔了抗卵菌綱殺菌劑約 50% 的市場，因此在製造時，常與其他抗卵菌綱殺菌劑製成混合劑，例如鋅錳右滅達樂、鋅錳克絕。這類多作用點抗卵菌綱殺菌劑目前無抗藥性族群報導。

結 論

國內作物及害物由於種類繁雜，因此在藥劑的使用上，往往有用了藥就會產生抗藥性的顧慮，然而產生抗藥性的因子，包括藥劑作用機制、藥劑使用與病原菌生物學等 3 個因子，並非單純的藥劑使用可造成抗藥性現象，因此在抗藥性風險評估時，必須對藥劑與病原菌配對進行考量，例如葡萄露菌抗 QoI 的族群在田間可迅速產生，而晚疫病菌對右滅達樂等苯醯胺類容易產生高抗性的抗藥性族群。對於卵菌綱殺菌劑使用，應將所有不同作用機制的殺菌劑輪替或混合使用，最佳施用時機應在病害發生初期使用，並嚴格遵循推薦之使用濃度及次數，如此可延緩或降低田間產生抗藥性族群的機會與速度，進而確保藥劑之使用壽命與效用。

國內對卵菌綱抗藥性研究，大都放在藥效及監測方面，少有對抗藥性產生機制進行深入研究，一方面是露菌、白銹菌屬絕對寄生菌，無法如疫病菌或猝倒病菌在培養基進行藥劑試驗，因此如何加強露菌、白銹菌等絕對寄生菌的抗藥性族群監測，開發抗藥性偵測技術，是未來應積極進行的重點，另一個問題，則是如何正確的評估田間抗藥性族群的分佈，以及強化卵菌綱引起的病害管理，是未來應強化研究的重點之一，使抗藥性問題，自偵測、監測、評估到管理形成一系統化的農藥研究主

軸，才能促進農藥的使用與管理更合理化，自然就達到對環境更友善的環境保護目的。

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Fungicidal Resistance of plant pathogenic Oomycetes

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Abstract

This review was based on decade research on the fungicidal resistance of plant pathogenic Oomycetes. The strategy of resistance management was also suggested in this article. Mode of action of Anti-Oomycete fungicides are mainly divided into r-RNA polymerase inhibitor, quinone outside inhibitor (QoIs), carboxylic acid amides (CAAs), cyanoacetamide-oxime etc. selective fungicides, and copper, mancozeb, chlorothalonil etc. multi-site fungicides. Recent researches were focused on the resistance genes and the monitor of resistance populations in the field. In the researches of resistance genes, resistance populations of *Phytophthora infestans* causing late blight of potato and tomato were highly resisted to mefenoxam (metalaxyl-*M*) phenylamide fungicides, therefore the resistance management of *P. infestans* was highly concerned in the potato producing area. Mode of action of QoIs was the inhibition of the mitochondrial respiration. Resistance of QoIs was induced when the position 143 of cytochrome *b* gene was mutated from GGT to GCT. Although resistance population of *Plasmopara viticola* was occurred quickly when QoIs applied in the field, they also decreased quickly when QoIs stop applying in the field, therefore the fungicidal risk of QoIs were medium. Resistance of CAAs was controlled by 2 nuclear recessive genes, although their mode of action was not fully elucidated, the fungicidal risk was classified from low to medium. Fungicidal resistance populations were monitoring yearly in European Union, and common fungicidal management recommendations were generated annually

by Working Groups of Fungicide Resistance Action Committee. Crops and pests were both diverse and complicated in Taiwan, for the management of fungicidal resistance in fields, the authorities should reinforce the systematic and long-term monitoring and survey projects, and according these results to generate the management strategy of fungicidal resistance in Taiwan.

Keywords: Oomycetes, *Phytophthora* spp., downy mildews, fungicidal resistance

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