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專題論述

水稻耐旱機制與分子育種策略之進展

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摘要

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水稻為全球重要主糧作物，對水資源需求高，面對日益嚴峻的氣候變遷與水資源短缺挑戰，提升其耐旱能力已成為確保糧食安全與實現農業永續發展的關鍵課題。本文綜述水稻在乾旱逆境下於生理、生化及基因層級的調控機制，涵蓋滲透調節、活性氧清除、氣孔調控及根系結構等核心途徑。近年學者透過數量性狀基因座 (qualitative trait loci; QTLs) 定位與候選基因選殖，已鑑定多個與耐旱性相關之關鍵基因與區域，包括 qDTYs、$qDTR_8$、$qDLR_{8.1}$、*OsNAC5*、*OsCPK9* 及 *LEA* 蛋白基因等，為分子育種提供重要遺傳資源。在小分子調控方面，已鑑定逾 30 種與乾旱反應相關的 miRNA，其中 19 種於植物乾旱反應期間，具有明確的調控功能，如 miR393、miR398、miR160、miR167 及 DST-amiRNA，分別參與生長素訊號、抗氧化能力及氣孔開閉等機制，構成一層關鍵的基因表現調控網絡。育種實務面，耐旱育種已逐步導入分子標記輔助選拔與 QTLs 堆疊 (pyramiding) 策略，成功育成多個具耐旱性狀之水稻品系。然而，乾旱外表型之田間表現與準確量化仍是主要的挑戰課題，限制了遺傳增益的進一步提升。未來應結合高通量表型體分析技術、基因體與表觀基因體資訊，整合環境數據進行乾旱反應之系統性解析，以建構多維度調控網絡與關鍵選拔指標，進而加速耐旱水稻品種之開發，以因應氣候變遷下的挑戰，並實現作物生產系統的智慧化與永續轉型。

關鍵詞：水稻、乾旱耐受性、數量性狀基因座、候選基因、分子育種。

前言

全球人口預估於2100年將超過100億 (Samir *et al*. 2024)。因此，『糧食安全』已是目前農業所面臨的最嚴峻挑戰 (Tiwari *et al*. 2024)。水稻是提供逾全球 1/3 人口的主要糧食作物，更是提供亞洲人 80% 日攝取熱量來源 (D'Odorico *et al*. 2014)。然而，水稻卻因為其較小根系統結構、較薄表皮蠟質及快速閉合之氣孔，導致其是一種乾旱敏感的作物 (Sahebi *et al*. 2018)。同時，受全球氣候變遷的影響，多數糧食作物生產區域面臨水資源的匱乏 (Liu *et al*. 2025)。雖然，臺灣年平均降雨量的長期趨勢未明顯減少，但全年各季節連續乾旱日數，卻因受氣候變遷的影響而變化 (Shanka *et al*. 2025)，造成近來乾旱災情不斷，尤其臺灣民間素有『三年一小旱、五年一大旱』的說法，在 2002–2020 年間，共發生 8 次旱災與 4 次大規模停灌休耕事件，對水稻產業的穩定生產構成重大挑戰 (Narvaez *et al*. 2022)。放眼亞洲地區，約有 340 萬公頃灌溉稻田與 80 萬公頃陸稻持續受到乾旱威脅，尤以近年受聖嬰現

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象影響，加劇乾旱面積持續擴大 (Singh *et al*. 2016; Hasan *et al*. 2025)。

在全球氣候變遷與水資源日益拮据的背景下，開發耐旱水稻品種已成為確保糧食安全與提升農業永續性的關鍵策略之一。儘管水稻耐旱育種早已展開，但受限於 2 大瓶頸：其一，缺乏具高耐旱潛力的種原資源；其二，尚未建立適用田間多樣環境的精準耐旱表型分析技術。過去，國際水稻研究所 (International Rice Research Institute; IRRI) 曾對數千份水稻種原進行篩選，卻僅有少數品種 (系) 具有明確的耐旱特性 (Singh *et al*. 2016)，顯示傳統評估方式可能難以解析耐旱性狀之複雜遺傳架構。實際上，水稻面對乾旱逆境時，在生理、生化乃至基因調控表現機制等層面上，展現多維度且複雜交互作用的機制，包括氣孔調節、滲透調節物質累積及抗氧化防禦系統啟動等 (Upadhyaya & Panda 2019; Gupta *et al*. 2020; Melandri *et al*. 2020; Ma *et al*. 2024)。如此多維度的調控網絡，使得水稻的耐旱特性恐難以由單一表型指標進行精準的篩選，進而導致育種家不易自田間篩選出具耐旱潛力基因型的品種 (系)。因此，建立整合生理、生化及分子標誌的耐旱性評估體系，將有助於精準選拔具育種價值的品種 (系)，並可加速耐旱關鍵選拔指標的開發與導入應用。爰此，本研究整合了水稻在形態、生理及分子層面的耐旱反應機制，並嘗試建立系統化的生理–分子關聯模型，以提供未來耐旱育種之理論依據。

水稻乾旱逆境之形態、生理及生化反應機制

水稻在乾旱逆境下，於形態外觀上常出現多種顯著變化：植株高度下降、分蘖數減少、葉片生命週期縮短、葉面積縮小、葉片捲曲 (leaf rolling; LR) 程度增加、根莖比提高及早熟現象加劇，最終導致整體生物量減少。研究指出，葉片機動細胞 (motor cells) 在失水後產生收縮，造成葉片向上捲曲；同時，葉片厚度、葉脈結構、維管束及束鞘細胞 (bundle sheath cells) 也發生明顯的形態變異 (Yan *et al*. 2020; Gunnula *et al*. 2022)。

於生理層級，乾旱會限制葉組織細胞的分裂與生長，誘導氣孔關閉，進而降低細胞內二氧化碳 (carbon oxidate; CO_2) 濃度，導致光合作用速率 (photosynthetic rate) 下降。伴隨著膨壓與滲透壓調控失衡及氧化逆境升高，也進一步抑制呼吸作用，最終削弱水分利用的效率。在生化層面，乾旱逆境會降低葉綠體基質中 1, 5-二磷酸核酮糖羧化酶/加氧酶 (ribulose-1,5-bisphosphate carboxylase/oxygenase; Rubisco) 酵素活性與淨光合作用能力，同時誘導一系列抗逆代謝物質的累積，包括脯氨酸 (proline)、多胺 (polyamines)、離層素 (abscisic acid; ABA) 及抗氧化酵素等，以協助植物維持細胞穩定性及防禦能力 (Oladosu *et al*. 2019)。整體而言，乾旱逆境會造成水稻光合產物的分配與轉運失衡，進而影響稻穗充實與穀粒形成，導致降低穀粒的重量與大小，甚至在嚴重條件下，會引發植株的死亡。

現行研究發現，植物乾旱抗性 (drought resistance) 可定義為有限水資源下仍能維持穩定產量的綜合能力。因此，性狀具有高度的複雜性，涉及多維度的形態、生理及代謝反應路徑。爰此，學者已將植物耐旱反應歸類為 3 大類型 (Kramp *et al*. 2022)，分別為：迴避 (avoidance)：指植物透過形態與生理調節，維持較高組織水勢，以避免細胞脫水。通常具備此機制的植物多具深根系、氣孔關閉敏感性高、LR 度高及葉片常綠且有較佳的呼吸效率；逃脫 (escape)：為植物在發生嚴重土壤缺水前，得快速完成生育週期的策略，其特徵包含：早開花、早熟、高葉氮水平、高光合作用能力及較佳的同化物再動員力等特性 (Liao *et al*. 2023)；耐性 (tolerance)：則是植物處於低量組織水狀態下的生存能力，包含：組織滲透調節能力、較高保護性的溶質、脯氨酸及耐旱逆境蛋白酶含量等，或較高的氣孔導度，或可維持一定的光合作用水平 (圖 1)。

上述分類機制不僅有助於釐清水稻耐旱的反應多樣性，更可作為耐旱性狀分子育種之重要指標基礎，進而促進耐旱基因型品種 (系) 篩選的重要參考。爰此，本節將進一步綜整水稻乾旱逆境時之外觀表型、生理及生化層面反

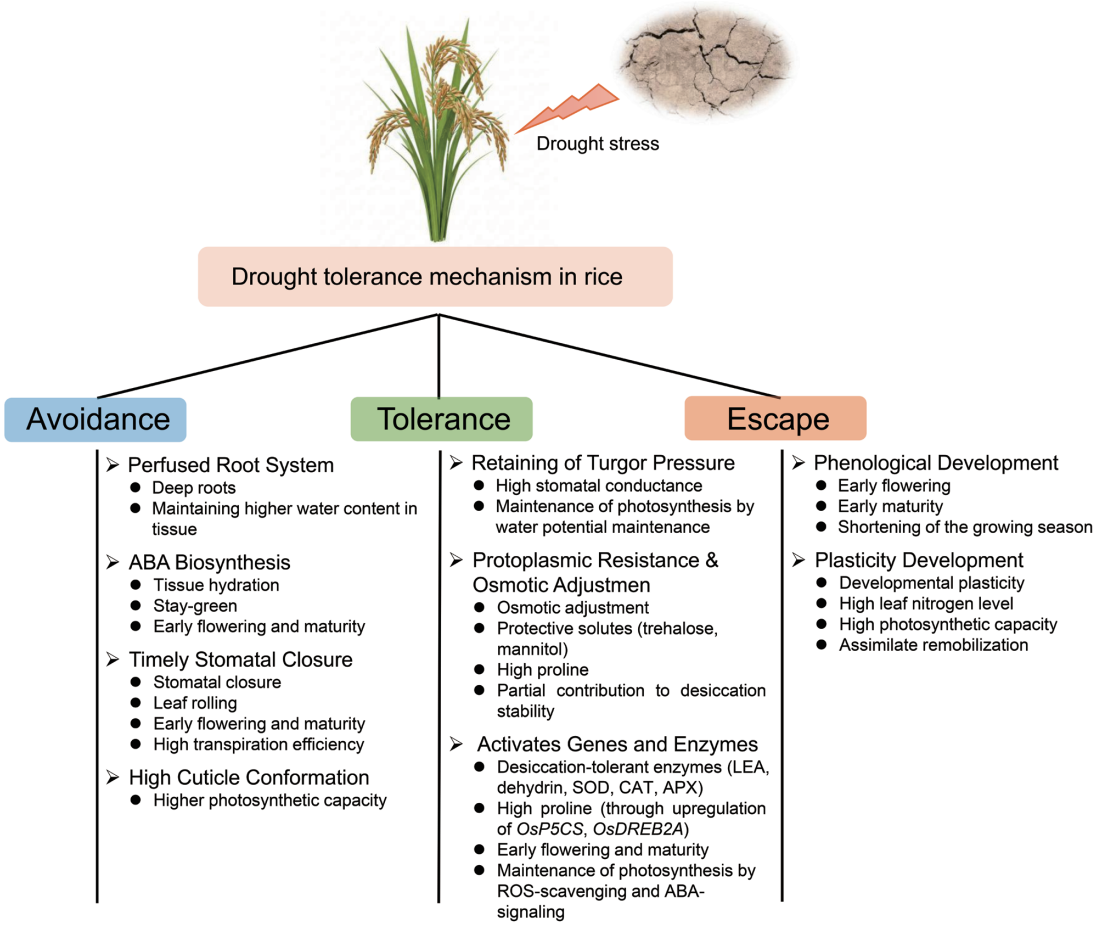


圖 1. 植物於乾旱逆境的反應。

Fig. 1. The responses of plants under drought stress. LEA: late embryogenesis abundant; SOD: Superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; *OsP5CS*: *Oryza sativa* delta-1-pyrroline-5-carboxylate synthase; *OsDREB2A*: *Oryza sativa* drought-responsive element binding protein 2A.

應機制，作為後續耐旱特性研究與相關分子育種策略的重要理論基礎。

水稻乾旱逆境下之型態與解剖構造變化

水稻葉片在乾旱逆境下的形態與解剖學的反應機制

乾旱逆境水稻植株因土壤水勢 (water potential) 的下降，導致木質部水分的傳輸受阻，致使葉細胞無法維持正常的膨壓 (turgor pressure)，進而抑制其生長與細胞擴張，導致劍葉顯著縮小 (Hussain *et al*. 2018)。水分供應的不足，不僅影響劍葉的正常發育，也改變其組織結構與超微形態，包括：葉面積縮小、氣孔密度減少、細胞壁增厚、角質層沉積增加，及維管傳導組織的發育異常 (Upadhyaya & Panda 2019)。在外觀表型上，LR 與劍葉早期衰老 (leaf senescence)，常被視為水稻對乾旱逆境的典型反應，亦是田間篩選耐旱品種 (系) 的重要外觀參考指標。此外，葉片諸多相關性狀，已被證實可反應水稻對乾旱的耐受能力，包括：劍葉面積 (flag leaf area)、葉面積指數 (leaf area index; LAI)、葉片相對含水量 (relative water content; RWC) 及葉片色素含量 (leaf pigment content) 等 (表 1)。這些性狀在

表 1. 葉片表型性狀指標與水稻耐旱特性的對照。

Table 1. Leaf phenotypic trait indices in relation to the drought tolerances of rice[z].

Indicator name	Definition	Physiological significance	Application in drought tolerance selection
Flag leaf area	Leaf area of the main panicle flag leaf (cm^2)	Determines photosynthetic potential and nutrient supply to the panicle	Larger flag leaf area enhances photosynthesis and grain filling under drought conditions
LAI	Total leaf area per unit ground area (m^2/m^2)	Reflects canopy light interception efficiency and transpiration capacity	Moderate LAI helps balance water use; overly high LAI may cause excessive water loss
RWC	(Fresh weight − Dry weight)/(Turgid weight − Dry weight) × 100%	Evaluates water retention ability of leaf tissues	High RWC indicates good water status and serves as an important drought tolerance indicator
LR	Longitudinal curling of leaves caused by decreased turgor pressure	Morphological adaptation to drought, reducing transpiration	Widely used for rapid field drought scoring (scale 1–9)
Leaf thickness and cell wall thickening	Leaf cross-sectional thickness and cell wall structural changes	Influences water retention and mechanical support	Thicker leaves delay water loss but must balance photosynthetic efficiency
Leaf pigment content (Chlorophyll)	Concentration of chlorophyll a/b and total pigments	Indicates photosynthetic capacity and leaf health status	Chlorophyll reduction is an early drought stress signal, useful for non-destructive monitoring
Early leaf senescence index	Rate of leaf chlorosis, yellowing, and necrosis	Reflects nutrient remobilization under drought	Indicates grain filling potential, positively correlated with drought tolerance
Stomatal density	Number of stomata per unit leaf area	Regulates gas exchange and water transpiration	Lower density reduces water loss, acting as a drought adaptation strategy
Cuticle development	Thickness of waxy and cuticular layers on leaf surface	Enhances resistance to water loss and mechanical protection	Closely related to drought avoidance strategies
Stomatal conductance	CO^2 and water vapor permeability influenced by stomatal aperture regulation	Balances photosynthesis and water loss	Key physiological parameter measured with precision instruments, can be integrated with genotype analysis

[z]LAI: leaf area index; RWC: relative water content; LR: leaf rolling; CO^2: carbon dioxide.

乾旱條件下可呈現顯著變異，並已建立評分分級系統，廣泛應用於水稻耐旱品種 (系) 之田間選拔與分子育種選拔策略 (Hirooka *et al*. 2017; Swapna & Shylaraj 2017; Kumar *et al*. 2021; Gunnula *et al*. 2022)。

水稻乾旱逆境下的根系形態與生理特性

作物根系的形態與功能，是乾旱逆境作物維持水分吸收與產量穩定的關鍵因子。而水稻面臨水分缺乏時，其產量的表現與根系構造特性及生長動態，有密切的關聯性。近來研究指出，根系多樣性 (如乾重或總長度) 可作為評估乾旱逆境水稻之生產潛力的預測指標 (Kim *et al*. 2020)，爰此已有學者進一步觀察不同水稻品種 (系) 在乾旱下的根系表型外觀反應，藉此評估其耐旱潛力與適應策略。另一方面，有學者發現，水稻在乾旱逆境下，根系會因 ABA 濃度的上升，誘導其根系加長，以提高深層土壤水分的吸收能力。整體而言，具備較深厚根系、粗壯主根、分支能力強及高根莖比 (root/shoot ratio) 等根系性狀的水稻品種 (系)，通常具有較佳的乾旱適應性與穩定產量 (Mishra *et al*. 2019; Kim *et al*. 2020; Ramachandran *et al*. 2021)。因此，水稻根系的形態與生理性狀，在乾旱逆境下，不僅影響水稻苗期的初始生長，亦與後期穀物產量的形成有密切關聯性，故是耐旱品種選拔的重要依據之一。

目前水稻根系的表型分析，多將根系區分為上部 (根冠至近地表層)、中部 (主根與次生根中段) 及下部 (主根延伸區與部分深層側根) 3 個根區，經取樣清洗乾淨後，再透過影像分析工具進行根性系統結構的量測。常見根系掃描與分析軟體，包括：WinRhizo、RhizoVision Explorer 及 ARIA (Automatic Root Image Analysis) 等 (Li *et al*. 2022)。這些工具可量化根長 (root length)、根表面積及根容積等重要參數，提供高通量且客觀地根系性狀量測的結果，有助於加速耐旱相關數量性狀基因座 (qualitative trait loci; QTLs) 探勘與輔助耐旱育種篩選等應用。

水稻乾旱逆境下之生理反應與細胞膜功能調控

乾旱逆境對水稻光合作用之效應

乾旱逆境會顯著削弱水稻的光合作用速率與氣體交換能力。當植株缺水時，葉片氣孔雖能藉閉合減少蒸散作用，但同時限制 CO_2 進入葉肉細胞，使 CO_2 同化速率下降。此限制造成電子傳遞鏈中電子累積，促使活性氧族 (reactive oxygen species; ROS) 生成，進一步引發光合組織氧化逆境 (Zhu *et al*. 2020)，並損害光合作用結構與功能，包括：光捕獲效率降低、Rubisco 之酵素活性減弱，以及葉綠素含量減少 (Panda *et al*. 2021)。對缺水敏感的水稻品種 (系) 而言，光合作用受限，加上根區水分利用率的下降，會造成顯著產量損失 (Gupta *et al*. 2020; Zhu *et al*. 2020)。在光系統層級，乾旱逆境會造成光系統 I (photosystem I; PSI) 與光系統 II (photosystem II; PSII) 運作的破壞，尤其 PSII 對電子傳遞與腺苷三磷酸 (adenosine triphosphate; ATP) 合成扮演著至關重要的角色。乾旱逆境會降低水稻光反應與氧氣釋放的效率，致使電子傳輸鏈受抑制並導致 PSII 失去活化 (Mishra *et al*. 2019)。

葉綠素作為光合作用的核心色素，負責捕獲光能並轉化為還原力。然而缺水會降低葉肉細胞對 CO_2 的利用潛力，減少活性葉綠素含量，並導致最大 PSII 量子產率 (Fv/Fm) 的下降 (Zhu *et al*. 2020; Guo *et al*. 2022; Arief *et al*. 2023)。此外，類胡蘿蔔素在光保護中亦扮演關鍵角色，不僅能吸收過量光能避免光抑制外，亦為多種逆境反應訊號分子的前驅物 (Swapnil *et al*. 2021)。因此，利用分子育種或基因工程提升作物的類胡蘿蔔素含量，已成為目前強化作物乾旱適應性或光保護能力的潛在策略 (Gao *et al*. 2023; Kumar & Sindhu 2024; Nazari *et al*. 2024)。

乾旱逆境對水稻細胞膜功能之效應

水稻與環境水分間的關係，常以水勢能 (water potential) 與 RWC 作為核心指標予以描

述 (Gupta *et al*. 2020)。其中，水分利用效率 (water use efficiency; WUE) 被視為水稻在水分逆境下決定產量潛力的關鍵組成因子，亦是提升水稻耐旱能力的重要策略之一 (Mishra *et al*. 2019)。RWC 則為評估水稻植株體內水分的最佳綜合性測量值，能反應植株體內水勢能與細胞膨壓的變化情形。當水稻暴露於乾旱逆境時，常呈現 RWC 下降、膨壓降低及蒸散作用受抑等負面生理效應 (Gupta *et al*. 2020)。在蛋白質體研究方面，有學者以 4 週齡耐旱水稻幼苗為材料進行篩選，發現供試材料在缺水處理 48–72 時期間，因脯氨酸含量上升而促進滲透調節，使 RWC 呈現穩定上升趨勢 (Medha *et al*. 2021)。脯氨酸在滲透調節中扮演關鍵角色，不僅有助於維持葉片膨壓，亦能減緩水分逆境對細胞功能的損害。

另一方面，細胞膜穩定性 (cell membrane stability; CMS) 於乾旱逆境下的維持，已被廣泛認為是植物耐旱性的重要生理指標。乾旱逆境會使膜系統的水分被排除，導致脂質結構受損與錯位，進而增加細胞膜的通透性，使植體在脫水過程中更易喪失細胞完整性 (Singh *et al*. 1992; ElBasyoni *et al*. 2017)。細胞膜穩定性指數 (membrane stability index; MSI) 可依據 Blum & Ebercon (1981) 的方法進行測定，而該指數已被應用於探討水稻在乾旱逆境下的膜穩定性與產量表現之間的相關性 (Blum & Ebercon 1981; Upadhyaya & Panda 2019)。

水稻乾旱逆境下之生化調節與抗氧化防禦系統

在乾旱逆境下，水稻可透過有機與無機滲透性溶質 (osmolytes) 的累積，減緩細胞內滲透壓，以維持細胞膨壓與基本生理功能。目前所發現的滲透保護劑包括：脯氨酸、甘氨酸甜菜鹼 (glycine betaine) 及各類可溶性糖。這些物質可透過滲透調節 (osmotic adjustment)，有效減緩脫水所造成的細胞損傷 (Kumar *et al*. 2017; Upadhyaya & Panda 2019)。另，細胞內蛋白質含量與組成的變化，配合抗氧化防禦系統的的活性提升，亦有助於強化水稻耐旱特性 (Pandey & Shukla 2015)。此外，學者亦發現有些植物激素，如 ABA、油菜素內酯 (brassinosteroids; BRs) 及乙烯 (ethylene)，於特定組織與時序的專一性表達，通常亦能有效促進植株的乾旱適應性，而不犧牲最終產量 (Gupta *et al*. 2020; Haghpanah *et al*. 2024)。

乾旱逆境下滲透物質的累積

滲透調節為植物耐旱的核心生理過程之一 (圖 1)。當葉細胞膨壓下降時，植株會誘導滲透保護劑累積，以維持水分平衡與細胞完整性。以玉米為例，缺水處理可誘導脯氨酸、可溶性糖、酚類化合物及總游離胺基酸等的累積，並顯著提升耐旱能力 (Anjum *et al*. 2017)。脯氨酸是一種五碳胺基酸，兼具滲透調節與保護細胞結構功能，亦可作為篩選耐旱品種 (系) 的生化標記 (Hayat *et al*. 2012; Pandey & Shukla 2015; Mishra *et al*. 2019; Medha *et al*. 2021)。糖類除作為能量與結構來源外，亦參與光合作用與呼吸作用的調控。在乾旱逆境中，水稻會累積雙醣、低聚醣、果聚醣等可溶性糖及特定糖醇，如甘露醇、山梨糖醇及海藻糖，並被證實能增強水稻的耐旱性 (Benkeblia 2022)。尤其，學者利用代謝體學研究分析發現，水稻於乾旱逆境下，會累積如脯胺酸 (proline)、海藻糖 (trehalose) 及棉子糖 (raffinose) 等滲透保護劑，同時伴隨 ABA 與茉莉酸 (jasmonic acid) 等信號分子的變化 (Alcázar *et al*. 2010; Kajrolkar 2025)。綜合而言，脯氨酸與可溶性糖的協同累積，是水稻在乾旱逆境維持生理活性的重要策略 (Upadhyaya & Panda 2019)。進一步整合蛋白質體學 (proteomics) 與代謝體學研究研究結果，學者發現乾旱逆境下的玉米，會調整其代謝過程，傾向於胺基酸與有機酸的分解代謝，以滿足在水分虧缺下的能量需求 (Witt *et al*. 2012)。而這些針對乾旱逆境下植物代謝重構的見解，可對未來進行靶向性代謝工程提高作物缺水耐受性，提供重要的關鍵基礎。

乾旱逆境下 ROS 的產生

ROS 為植物有氧代謝的天然副產物，但於乾旱逆境下，其生成速率顯著增加，將對細胞造成氧化損傷。ROS 主要在光合作用與呼吸作用過程中，分別於葉綠體與粒線體中

所產生 (Gill & Tuteja 2010)。然而，乾旱逆境會抑制植物細胞的電子傳遞鏈，導致超氧自由基 (superoxide; $O_2^{\bullet-}$)、過氧化氫 (hydrogen peroxide; H_2O_2) 及羥基自由基 (hydroxyl radical; OH•) 的大量累積 (Melandri *et al*. 2020; Fathi *et al*. 2025)。過量 ROS 進而會氧化蛋白質、脂質及 DNA，造成光合作用與光呼吸的破壞，並引發脂質過氧化與細胞膜結構的崩解，最終導致細胞死亡 (圖 2) (Melandri *et al*. 2020; Fathi *et al*. 2025)。因此，降低 ROS 產生與增強抗氧化系統則是另一提升水稻耐旱性的關鍵策略。

乾旱逆境下抗氧化物質的角色

植物具備複雜的抗氧化防禦系統，可分為酶類抗氧化物與非酶類抗氧化物 2 大類 (Gill & Tuteja 2010；圖 2)。其中，酶類抗氧化物包括：超氧化物歧化酶 (superoxide dismutase; SOD)、過氧化氫酶 (catalase; CAT)、穀胱甘肽過氧化物酶 (glutathione peroxidase; GPX)、抗壞血酸過氧化物酶 (ascorbate peroxidase; APX)、單脫氫抗壞血酸還原酶 (monodehydroascorbate reductase; MDHAR)、脫氫抗壞血酸還原酵素 (dehydroascorbate reductase; DHAR) 及穀胱甘肽還原酶 (glutathione reductase; GR)；非酶類

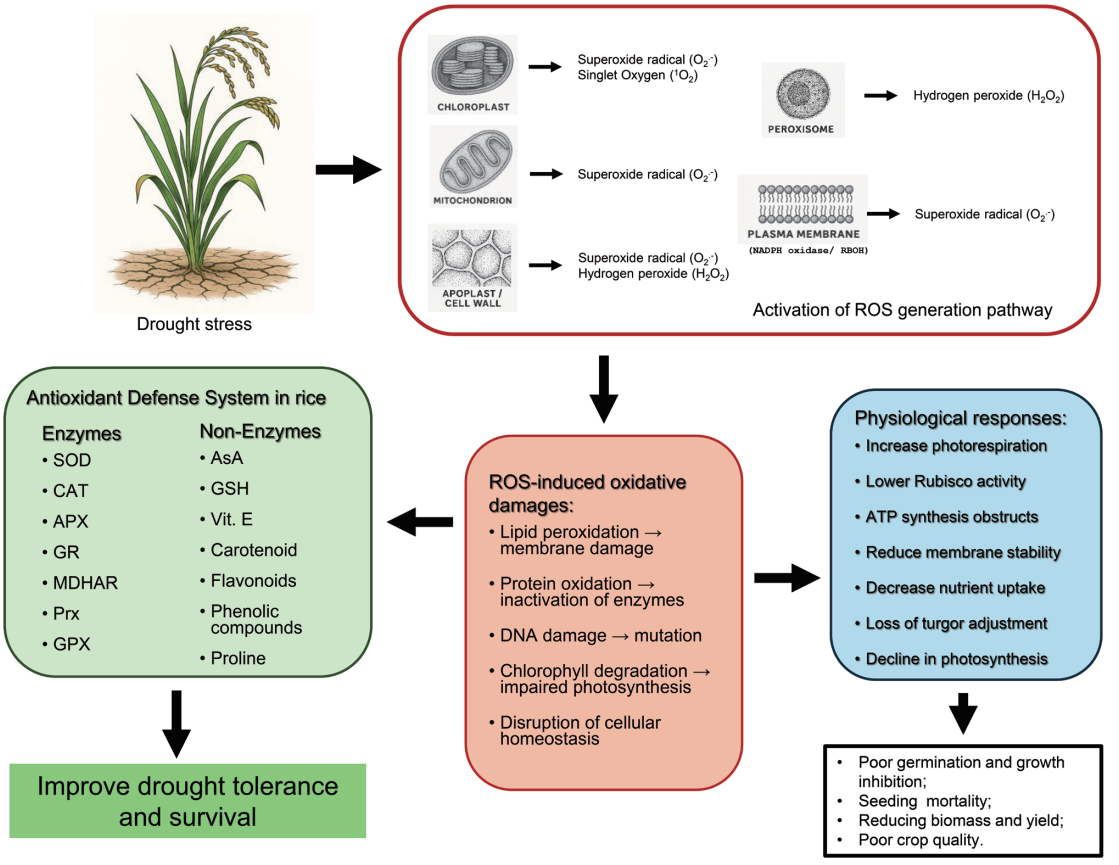


圖 2. 水稻乾旱逆境之活性氧族所造成的損害及其抗氧化防護機制。

Fig. 2. Reactive oxygen species (ROS)- induced cellular damage and antioxidant defense mechanisms in rice under drought stress. SOD: superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; GR: glutathione reductase; MDHAR: monodehydroascorbate reductase; Prx: peroxidases; GPX: guaiacol peroxidase; AsA: ascorbic acid; GSH: glutathione; Vit. E: vitamin E; ATP: adenosine triphosphate.

抗氧化物包括：抗壞血酸 (ascorbic acid; AsA) 與穀胱甘肽 (glutathione; GSH)。SOD 是 ROS 清除的第一道防線 (Gill & Tuteja 2010)，在乾旱逆境處理的水稻與小麥植株，常誘導其活性的上升 (Csiszar *et al*. 2005; Zlatev *et al*. 2006; Lü *et al*. 2010; Mishra & Panda 2017; Melandri *et al*. 2020)。CAT 負責分解過氧化氫，水稻於乾旱逆境下可調整其活性，但活性下降是水稻對多種逆境的常見反應 (Qureshi *et al*. 2018)；GPX 則可有效清除氧化氫，其活性已被當作水稻耐旱的重要指標 (Bhattacharje & Dey 2018; Qureshi *et al*. 2018; Bhandari *et al*. 2023)。

位於葉綠體的 AsA–GSH 循環 (圖 2) 是過氧化氫清除的核心路徑，關鍵酶如 APX 與 GR 在乾旱下活性增強，有助於維持細胞氧化還原平衡並增強植物抗旱特性 (Bhattacharjee & Dey 2018; Upadhyaya & Panda 2019; Fathi *et al*. 2025)。增加 AsA 與 GSH 含量與耐旱性間具有高度的關聯性，其已被證實可有效降低乾旱所造成的產量損失 (Bhattacharjee & Dey 2018; Melandri *et al*. 2020)。因此，強化抗氧化代謝相關酶類與非酶類成分的表現，已成為耐旱水稻分子育種的重要策略之一。

植物耐旱分子調控機制

植物對乾旱的反應涉及多維度的複雜訊號傳遞：自細胞膜受器感知乾旱逆境後，透過訊息傳導，啟動耐旱相關基因的表現 (圖 3；Dash *et al*. 2018; Oladosu *et al*. 2019; Sonowal *et al*. 2025)。由於耐旱性狀複雜，致傳統雜交與選拔程序，常難以精確評估育種族群的耐旱特性。但分子標記技術則可提高篩選效率，或可應用於耐旱種原或品種的選拔。因此，研究者須致力於建立與耐旱相關的 QTLs (Barik *et al*. 2019; Upadhyaya & Panda 2019)，並配合發展田間自動化高通量的耐旱外表型分析方法 (Prakash *et al*. 2019)。

水稻耐旱 QTLs 定位研究現況與限制

QTLs 指在基因組上控制連續變異 (數量性狀) 的基因座。過去分子遺傳研究已在不同遺傳族群、生長階段與環境條件下，探勘出多個與乾旱相關的典型 QTLs (見表 2)，例如與產量、收穫指數、葉片含水量、捲葉度及稔實率相關者 (Alexandrov *et al*. 2015; Todaka *et al*. 2015; Dixit *et al*. 2017; Barik *et al*. 2019)。其中，連結產量表現的耐旱 QTLs (如 qDTYs、$qDTR_8$ 及 $qDLR_{8.1}$ 等)，在實務育種上備受重視，常與簡單序列重複 (simple sequence repeat; SSR) 等共顯性標記緊密連鎖，可用於早期世代的耐旱基因型篩選 (Mishra *et al*. 2013; Dixit *et al*. 2014; Ramchander *et al*. 2016; Singh *et al*. 2016; Dixit *et al*. 2017; Vinod *et al*. 2019; Venkateshwarlu *et al*. 2025)。此外，Barik *et al*. (2019) 更發現 qLR9.1 等 QTLs 可控制乾旱下的卷葉、乾重、收穫指數、穗花稔實率及含水量等性狀，顯示其在耐旱育種上具有高度應用潛力 (Barik *et al*. 2019)。

但目前多數已發表 QTLs 遺傳區間的距離仍較大，或有遺傳累贅的問題，或因其性狀解釋力深受環境影響，且其上關鍵基因尚未被選殖，均嚴重影響這些 QTLs 在耐旱育種選拔程序上的應用性 (Singh *et al*. 2016)。因此，未來或可進一步將相關 QTLs 進行細定位，或結合高通量自動化表型體 (automative phenomics) 分析技術與多環境田間試驗驗證，應是水稻耐旱特性研究由實驗室證據走向育種落地的關鍵。

現已選殖水稻耐旱基因

乾旱可誘導水稻發生大規模轉錄變化：約有 5,000 個基因上調表現，6,000 個下調表現 (Bin Rahman & Zhang 2016; Joshi *et al*. 2016)。現已知耐旱基因可分為 3 類 (見表 3 與圖 3)，彼此交互作用而共同塑造乾旱下的水稻生理/生化反應：(1) 膜轉運相關：調節離子/溶質運輸與滲透調節，支撐葉片含水與細胞膨壓維持；(2) 訊號轉導相關：包含 *CDPK* (calcium-dependent protein kinase) 與 *CIPK* (CBL-interacting protein kinase) 等，整合鈣訊號、ABA 及 ROS 的穩定狀態，快速驅動下游反應 (如 *CDPK7* 與 *CIPK03/12* 等) (Sahebi *et al*. 2018; Bandurska 2022)；(3) 轉錄調控相關：如 *DREB*/*CBF*、*NAC* 及 *WRKY* 等家族，

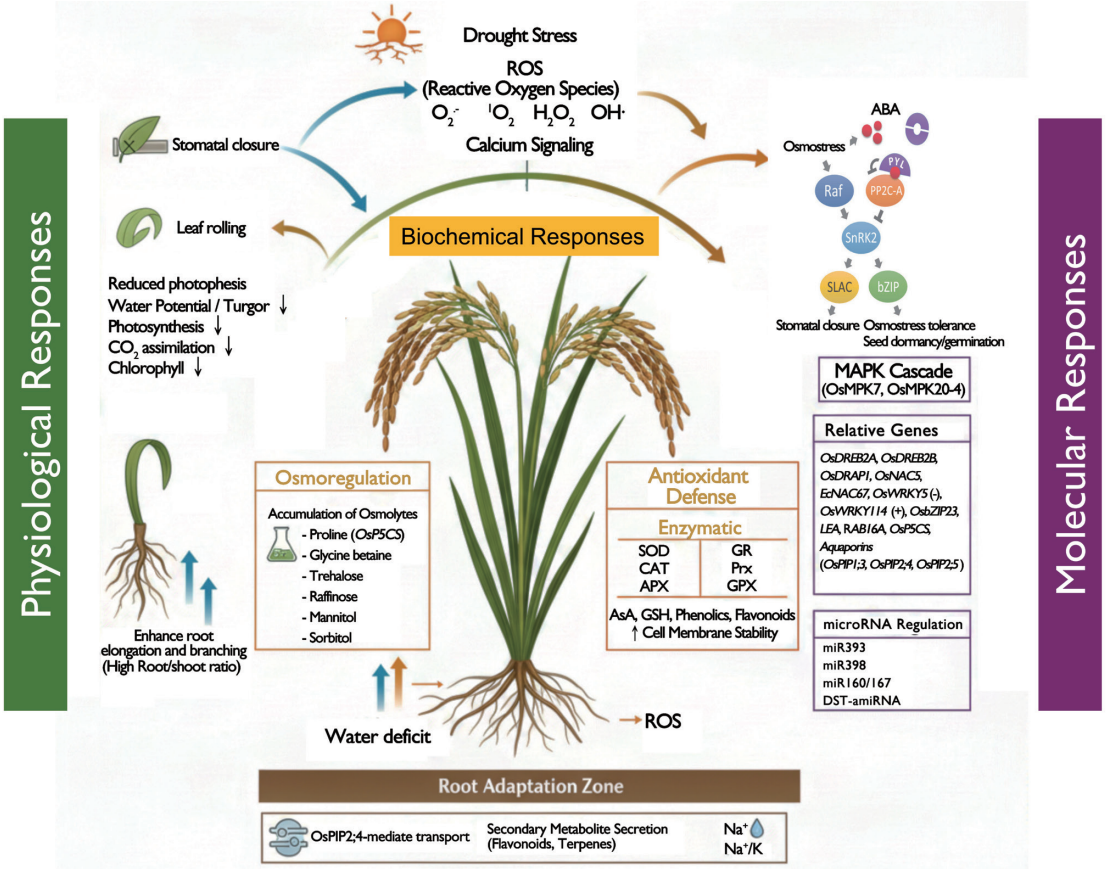


圖 3. 水稻在乾旱逆境下生理、生化與分子層次反應。

Fig. 3. The physiological, biochemical, and molecular responses of plants to drought stress. SOD: superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; GR: glutathione reductase; MDHAR: monodehydroascorbate reductase; Prx: peroxidases; GPX: guaiacol peroxidase; AsA: ascorbic acid; GSH: glutathione; OsMAPK7: *Oryza sativa* mitogen-activate protein kinase 7; OsMAPK20-4: *Oryza sativa* mitogen-activate protein kinase 20-4; *OsDREB2A*: *Oryza sativa* drought-responsive element binding protein 2A; *OsDREB2B*: *Oryza sativa* drought-responsive element binding protein 2B; *OsDRAP1*: *Oryza sativa* drought responsive AP2/EREBP 1; *OsNAC5*: *Oryza sativa* NAC-type transcription factor 5; *EcNAC67*: *Eleusine coracana* NAC transcription factor 67; *OsWRKY5*: *Oryza sativa* WRKY transcription factor 5; *OsWRKY14*: *Oryza sativa* WRKY transcription factor 14; *OsbZIP23*: *Oryza sativa* basic leucine zipper 23; *LEA*: late embryogenesis abundant gene; *RAB16A*: responsive to ABA gene 16A; *OsP5CS*: *Oryza sativa* delta-1-pyrroline-5-carboxylate synthase; *OsPIP1;3*: *Oryza sativa* plasma membrane intrinsic protein 1;3; *OsPIP2;4*: *Oryza sativa* plasma membrane intrinsic protein 2;4; *OsPIP2;5*: *Oryza sativa* plasma membrane intrinsic protein 2;5.

直接或間接調控抗逆效應基因之表達 (Dash *et al*. 2018; Upadhyaya & Panda 2019; Gupta *et al*. 2020; Kim *et al*. 2020)。

目前已被驗證的水稻耐旱功能性基因包括：*LEA*、*OsDREB2B* 及 *OsDRAP1* 等基因，可促進滲透調節保護與根系適應 (Dash *et al*. 2018)；在對伊拉克水稻品種的乾旱耐受性評估中，耐旱性最強的品種 'Mashkab' 顯示具有較高的 *OsDREB2A* 表現，暗示 *OsDREB2A* 表達與水稻耐旱性之間存在潛在關聯 (Al Azzawi *et al*. 2020; Gammanpila *et al*. 2025)。另一方面，*OsDREB2A* 的大量表現，已在轉譯層面證實能增強水稻的耐旱性 (Cui *et al*. 2011; Gammanpila *et al*. 2025)；*OsPYL/RCAR5* 與 *EcNAC67* 可提升根與芽之生長動態 (Rahman *et al*. 2016; Kim *et al*. 2020)；*OsNAC5* 則可促進水稻提高 WUE、

表 2. 水稻已發表之與耐旱相關的數量性狀基因座。

Table 2. The published drought-related quantitative trait loci (QTLs) in rice.

QTL	Chromosome	Marker interval	Parents	Associated traits	Reference
$qDTY_{1.1}$	1	RM431-RM104	Dhagaddeshi × Swarna	Grain yield and stem dry weight under drought	Venkateshwarlu *et al*. (2025)
$qDTY_{2.1}$	2	RM154-RM324	Aus × IR64	Grain yield and days to heading under drought	Sandhu *et al*. (2014)
$qDTY_{2.2}$	2	RM211-RM263	Kali Aus/2 × MTU1010	Grain yield under drought	Sandhu *et al*. (2014)
$qDTY_{2.3}$	2	RM263-RM573	Kali Aus/2 × MTU1010	Grain yield under drought	Palanog *et al*. (2014)
$qDTY_{3.1}$	3	RM168-RM468	TDK1 × IR55419-04	Grain yield under drought	Dixit *et al*. (2014)
$qDTY_{3.2}$	3	RG191-RM546	Danteshwari × Dagaddeshi	Grain yield under drought	Panda *et al*. (2021)
$qDTY_{6.1}$	6	RM168-RM468	TDK1 × IR55419-04	Grain yield under drought	Dixit *et al*. (2014)
$qDTY_{8.1}$	8	RM339-RM210	Swarna × Basmati 334	Grain yield and grain number under drought	Venkateshwarlu *et al*. (2025)
$qDLR_{8.1}$	8		IRAT109 × Yuefu	Leaf rolling	Qu *et al*. (2008)
$qDTR_{8}$	8	RM264-RM20a	Norungan × TKM9 BC_1F_5	Drought response index (composite)	Ramchander *et al*. (2016)
$qLR_{9.1}$	9	RM316-RM257	CR 143-2-2 × Krishnahamsa F_7	Leaf rolling, leaf drying, relative water content, spikelet fertility, harvest index	Barik *et al*. (2019)
$qDTY_{12.1}$	12	RM28166-RM28199	IR74371-46-1-1 × Sabitri	Grain yield under drought	Mishra *et al*. (2013)

表 3. 水稻基因組中已選殖之耐旱功能性基因。

Table 3. The cloned functional genes related with drought-response in rice genome.

Gene name	Gene source	Promoter	Transgenic construct[z]	Associated drought-related traits	Accession number	Reference
OsLEA3-1	Rice	HVA1/ CaMV 35S/ actin	OE	Increased yield	LOC_Os05g46480	Xiao *et al*. (2007)
CIPK03/CIPK12	Rice	Ubiquitin	OE/RNAi	Regulatory protein, signal transduction, protease; RNAi lines showed reduced fertility	AK072868 (AP003757); AK101442 (AP003409)	Xiang *et al*. (2007)
CDPK7	Rice	CaMV 35S	OE	Regulatory protein, signal transduction, protease	AB042550	Saijo *et al*. (2000)
OsITPK2/DSM3	Rice	CaMV 35S/ Ubiquitin	OE/amiR	Low fertility, reduced biomass	LOC_Os03g12840	Du *et al*. (2011)
OsDREB2A	Rice	4ABRC	OE	Enhanced survival rate of transgenic plants	Os01g0165000	Zhang *et al*. (2013)
OsNAC5	Rice	RCc3/ GOS2	OE	Increased root diameter, improved yield	AK102475	Jeong *et al*. (2013)
OsCPK9	Rice	CaMV 35S	OE	Enhanced stomatal closure for improved drought resistance and better osmotic adjustment in transgenics	LOC_Os03g48270	Wei *et al*. (2014)
OsPYL/RCAR5	Rice	GUS	OE	Inhibits growth	Os05g12260	Kim *et al*. (2014)
EcNAC67	Millet	RD29	OE	Increased relative water content, delayed leaf rolling, higher root and shoot biomass	KU500625	Rahman *et al*. (2016)
MAPK gene family	Rice	Ubi	OE	Regulatory protein, signal transduction		Huang *et al*. (2021a)
WRKY gene family	Rice	CaMBP/ CRSSP	OE/OX	Relative yield reduction		Raineri *et al*. (2015); Huang *et al*. (2021a); Lim *et al*. (2022); Song *et al*. (2022); Li *et al*. (2025)
OsPIP gene family	Rice		OE	Regulatory protein, signal transduction, and better osmotic adjustment		Verma *et al*. (2020); Bai *et al*. (2021); Huang *et al*. (2021b); Sun *et al*. (2021); Tong *et al*. (2025); Tran *et al*. (2025)

[z] OE: over expression; RNAi: RNA interference; amiR: artificial miRNA; OX: knock out.

光合作用及抗氧化酵素活性 (Khan *et al*. 2025)；水稻 *NAC* 轉錄因子家族透過調控與光合作用效率及碳同化相關的基因，在水稻面對多樣環境挑戰時扮演了優化碳固定的角色 (Gammanpila *et al*. 2025)；*OsCPK9* 可促進水稻強化氣孔關閉動力學；*OsDREB2A* 增強水稻乾旱與鹽逆境下的存活率 (Liu *et al*. 2014)；*OsP5CS* 表達增加有助於植物產生更多的脯氨酸，從而使植物免受乾旱影響 (Saddique *et al*. 2020)；*WRKY* 與 *OsITPK2* 亦參與水稻耐旱反應訊號整合與 ROS 平衡 (Du *et al*. 2011; Sahebi *et al*. 2018)；此外，水稻 *WRKY* 轉錄因子在調控水稻耐旱性方面展現出多重且複雜的機制，特別是其對 ABA 訊號、ROS 穩態及氣孔性能的影響 (Li *et al*. 2025)；*OsWRKY5* 負向調控 *OsMYB2* 的表現，進而抑制多個乾旱反應基因，包括 *OsLEA3*、Os*RAB16A* 及 *OsDREB2AI* 表現，而負調控水稻的耐旱反應 (Lim *et al*. 2022)。另一方面，*MAPK* 蛋白基因 (*OsMPK7*、*OsMPK9*、*OsMPK20-1* 及 *OsMPK20-4*) 可活化 *OsWRKY55* 的表現，進而加速植物體的水分流失與活化氧族累積 (Huang *et al*. 2021a)。此外，大量表現 *OsWRKY114* 亦會抑制 ABA 受體基因—*OsPYL2* 與 *OsPYL10* 的表現，進而限制氣孔的關閉 (Song *et al*. 2022)。

水稻中的水通道蛋白 (aquaporins; AQPs) 是水稻調控水分運輸的關鍵膜蛋白，對乾旱、鹽分及高溫逆境下的植株適應性，具有非常重要的角色 (Tong *et al*. 2025)。尤其，特定 AQPs 亞家族成員在耐旱機制中，是非常重要的，例如 *OsPIP2* 亞家族成員 (如 *OsPIP2;2*、*OsPIP2;3* 及根特異性表達的 *OsPIP2;4*) 能顯著提高水分吸收與運輸效率 (Bai *et al*. 2021; Sun *et al*. 2021; Tran *et al*. 2025)。其中，*OsPIP2;4* 甚至兼具運輸水分與非選擇性 Na^+、K^+ 離子的功能，有助於滲透調節 (Tran *et al*. 2025)。此外，在耐旱品種中，多個 AQPs 基因，包括：*OsPIP1;3*、*OsPIP2;4*、*OsPIP2;5*、*OsTIP2;1* 及 *OsNIP2;1*，在乾旱時會更強烈地協同增加表現量，顯示水稻的耐旱性是一種由多基因決定的複雜性狀 (Verma *et al*. 2020)。進一步利用 CRISPR/Cas9 準基因編輯技術，針對 *OsPIP1* 基因族進行多重編輯，證實了這些 AQPs 基因在維持滲透穩態中的關鍵作用 (Huang *et al*. 2021b)。目前這些基因大多於溫室或控環環境中被證實具耐旱效益，但要達到育種可信的增益，仍需在多點多年田間試驗結合表型體與環境共變量進行驗證，並評估其對產量構成與資源分配的長期影響。

microRNA 在水稻乾旱耐性的角色

miRNA 是一類小型非編碼 RNA，透過轉錄後抑制調控系統性的乾旱反應相關基因，水稻中已報導多條 miRNA 與乾旱功能相關 (Singh *et al*. 2020)。研究顯示，miR393、miR319 及 miR397 在乾旱下上調表現 (Sunkar & Zhu 2004)；miR393 透過調控 *OsAUX1* 與 *OsTIR1* 影響分蘖、開花期及生長素反應 (Xia *et al*. 2012)。水稻中另已發現逾 30 種與乾旱相關的 miRNA，19 種參與乾旱調控 (Zhou *et al*. 2010)；在 'Nagina 22' (N22) 中更鑑定 71 種新型 miRNA，顯示遺傳背景對 miRNA 網絡的調控表現作用顯著 (Mutum *et al*. 2016)。特定 miRNA，如 miR398 調控 *Cu/ZnSOD*，影響抗氧化能力 (Balyan *et al*. 2017; Lu *et al*. 2022)；miR160/miR167 作用於 *ARF*，參與早期生長素訊號與根系建構 (Upadhyaya & Panda 2019)。其他如 DST-amiRNA 與 ROS 穩定狀態相關基因，能促進氣孔關閉與密度下降，增強耐旱性 (Faisal *et al*. 2017)。miR169-3p 與 miR166e-3p 則與根系發育及碳水化合物代謝有關。這些 miRNA 為解析水稻耐旱機制與發展分子育種提供了關鍵工具與潛力標的 (Cheah *et al*. 2015; Upadhyaya & Panda 2019; Singh *et al*. 2020)。

多體學研究在乾旱逆境研究中的最新進展

多體學 (multi-omics) 研究策略是整合不同維度分子體學數據的系統生物學方法，可用來全面剖析植物於乾旱逆境下的分子與生理機制，進而為未來氣候適應型作物 (climate-resilient crops) 的育種工作，提供精準研究與應用路徑的基礎。其核心理念是透過基因體、轉錄體、蛋白體、代謝體、脂質體、離子體及表觀體等，各種體學資料的整合分析，進而描繪出植物乾旱反應的系統性網絡 (system-level drought response network；圖 3)，進而連結基

因調控、代謝重構及表型表現之間的層級關係 (Gupta *et al*. 2023; Goche *et al*. 2025; Kajrolkar 2025; Sonowal *et al*. 2025)。

透過高通量基因體與轉錄體的整合分析，可明確勾勒出植物耐旱性狀的多基因特徵與調控邏輯。尤其，全基因組關聯研究 (genome-wide association study; GWAS) 與功能基因體學的進展，使得研究者能深入研究植物耐旱關鍵突變位點與基因調控網絡。學者結合長片段測序 (long-read sequencing; LRS) 與單倍型解析 (haplotype phasing) 分析結果，可精準定位耐旱 QTL 區段，並預測候選基因的表達模式 (Yadav *et al*. 2019; Shinozaki & Yamaguchi-Shinozaki 2022)。此外，可利用基因編輯技術 (如 CRISPR/Cas9 與 prime editing)，針對耐旱相關調控因子，如 *DREB*、*NAC* 及 *bZIP* 家族基因，進行功能驗證，證實其在耐旱性狀扮演重要角色外，亦初步實現作物耐旱性狀的定向改造 (targeted improvement; Kajrolkar 2025)。

在水稻轉錄體與代謝體整合分析結果發現，乾旱逆境可誘導水稻 *OsDREB1C*、*OsNAC6* 及 *OsPP2C*，並重新平衡碳水化合物代謝與 ROS 代謝，強化細胞之能量穩態與抗氧化防禦 (Goche *et al*. 2025)。同時，在玉米與小麥乾旱逆境的轉錄體及代謝體的分析結果，亦發現能量轉換與滲透壓調節代謝路徑的重塑，應是植物的主要乾旱逆境反應模式 (Hashiguchi & Komatsu 2016)。此外，蛋白質體學通過質譜技術，呈現蛋白質豐度與轉譯後修飾 (post-translational modifications)，如磷酸化與蛋白質–蛋白質交互作用 (protein-protein interactions) 的動態變化，並發現 MAPK (mitogen-activated protein kinases) 訊息路徑、離層素相關調控 (ABA-dependent regulation) 及脂質重構 (lipid remodeling)，在植物乾旱逆境反應中，互為支撐 (Todaka *et al*. 2015; Kim *et al*. 2022; Li *et al*. 2023)。此類多維度跨體學資料的整合，使研究者得以建立分子訊號 – 代謝反應 – 表型表現的連續鏈結，為後續抗旱育種提供可量化之生物標誌 (biomarkers)。

同時，多體學亦揭露植物藉由多層次調控，進行代謝重構 (metabolic reprogramming)，以維持逆境下的內穩態 (homeostasis) (Lisec *et al*. 2006)。在水稻代謝體分析，顯示胺基酸 (如脯胺酸及丙胺酸 (alanine)) 及糖醇類 (如山梨醇 (sorbitol)、甘露醇 (mannitol)) 均大量累積，並參與滲透保護與 ROS 的清除 (Saddique *et al*. 2020)。蛋白體資料亦顯示，植物乾旱逆境下，其熱休克蛋白質、SOD 及 APX 等抗氧化相關蛋白質之上調，有助於減輕膜脂過氧化與光合抑制 (Goche *et al*. 2025)。蛋白質體與脂質體學 (lipidomics) 研究顯示，在乾旱下磷脂 (phospholipids) 比例上升、三酸甘油脂 (triacylglycerols) 降低，可維持細胞膜流動性與訊號傳導效率 (Liu *et al*. 2021)。同時，離子體研究發現鉀、磷及鋅等離子濃度與氣孔導度及抗氧化酵素活性呈正相關，顯示其在乾旱下扮演離子穩定器角色。此外，單細胞轉錄體學 (single-cell transcriptomics) 研究指出，乾旱逆境下特定細胞 (如保衛細胞或根尖細胞) 的分子多樣性與調控網絡表現差異顯著，證明細胞型特異性 (cell-type specificity) 為耐旱關鍵 (Netla *et al*. 2023; Sonowal *et al*. 2025)。

儘管目前多體學為植物乾旱反應研究提供新的契機，但其在資料處理與跨維度的整合仍面臨挑戰。首先，不同維度體學間的表現時間延遲效應與資料異質性，使得個體學間因果關係的預測更為複雜化 (Fukushima *et al*. 2009; Hasin *et al*. 2017)。其次，植物乾旱反應具有顯著的基因型 × 環境交互作用，造成不同族群間難以建立穩定模型 (Velten & Stegle 2023)。同時，現有多體學研究資料多為室內或溫室條件下所得結果，可能與實際田間表現的情形存有差距 (Fukushima *et al*. 2009; Hasin *et al*. 2017; Sonowal *et al*. 2025)。未來，或可整合下列策略，予以克服上述課題：(1) 整合 AI (artificial intelligence) 輔助多體學分析：結合機器學習與深度網絡 (CNN (convolutional neural network), GNN (graph neural network)) 模型，以辨識非線性基因 – 環境關係；(2) 時空層級體學分析 (spatiotemporal omics)：利用空間轉錄體學 (spatial transcriptomics) 追蹤抗旱細胞群動態；(3) 表型體 - 多體學聯結：結合高通量影像與組學資料，建立基因型 – 表型 – 環境 (G-P-E) 關聯模型；(4) 資料標準化與共

享：統一格式化標註與跨平臺數據標準，促進多研究間比較與再利用 (Goche *et al*. 2025; Sonowal *et al*. 2025)。

耐旱性育種應用現況：分子標誌輔助選拔與品種開發實例

為因應日益頻繁乾旱與匱乏水資源的挑戰，水稻耐旱育種已成為全球水稻生產穩定性的重要課題。透過前述水稻耐旱數量基因座定位與功能基因的選殖，研究者得以發現與耐旱關鍵 QTLs 與候選基因，並結合分子標記輔助選拔 (marker-assisted selection; MAS) 技術，有效導入至現行水稻商業品種。然而，多數耐旱育種相關計畫，有效耐旱品種開發的成功率仍偏低，主要受限於耐旱基因來源、多變的環境條件及目標導入品種的複雜遺傳背景 (Dixit *et al*. 2017; Barik *et al*. 2019; Singh *et al*. 2020; Kumar *et al*. 2021)。

國際耐旱品種開發的成功案例

IRRI 在過去十餘年積極導入耐旱 QTLs 堆疊策略，應用多個耐旱效益 QTLs，導入傳統高產品種，以提升其在乾旱逆境下的穩定產量表現。其中，qDTY 系列 QTLs 尤具代表性：(1) 育種家已成功將 $qDTY_{9.1}$ 導入至大面積栽培之高產品種—‘IR64’，實現對乾旱逆境的適應力提升 (Singh *et al*. 2016)；(2) Shamsudin *et al*. (2016) 成功透過分子輔助育種技術將 3 個耐旱 QTLs ($qDTY_{2.2}$、$qDTY_{3.1}$ 及 $qDTY_{12.1}$) 導入馬來西亞水稻品種 ‘MR219’，有效強化其在乾旱條件下的穩定生產力 (Shamsudin *et al*. 2016)；Dixit *et al*. (2017) 亦堆疊 3 個 QTLs ($qDTY_{3.1}$、$qDTY_{6.1}$ 及 $qDTY_{6.2}$)，開發於乾旱條件下具有高產特性的水稻品種—‘TDK1’ (Dixit *et al*. 2017)。

過去商用品種的應用限制與未來需求

早期推薦於灌溉田種植的 ‘Swarna’、‘Sambamahsuri’ 及 ‘IR36’ 等大多數高產品種，已被應用於耐旱育種計畫作為耐旱性狀的接收親本。尤其，當農民於降雨生態系統中種植這些品種時，若遭遇頻繁乾旱期，將因這些高產品種不具耐旱的特性，而造成嚴重的產量損失 (Hao *et al*. 2018)。然而，因過去未能針對乾旱適應性，建立有效測量與篩選方法，導致高產品種在實際耐旱環境中表現落差的主因之一。未來耐候水稻育種的核心挑戰，將不僅侷限於提升產量，更需聚焦於高產與耐旱性之協同育成，同時兼顧其對氣候變異與多重逆境 (multi-stress) 條件的適應能力。這包括：(1) 廣域適應性育種：針對不同氣候區域，建立多環境試驗體系，確保所選材料在多樣場域仍具穩定表現；(2) 應用高通量表型分析技術：建立客觀、量化且田間可操作的乾旱耐性指標，提升耐旱性狀的量測效率與選拔精準性；(3) 跨維度資料整合應用：結合 QTLs、候選基因、miRNA 及表型體數據，透過 AI 分析與機器學習模型發展新一代選拔策略，突破傳統單性狀選拔限制。

結語

水稻耐旱改良育種必須同時解決耐旱機制複雜、耐旱基因受環境強制約及耐旱外表型選拔指標不足等三項關鍵瓶頸。在耐旱機制部分，現學界已完成形態 – 生理 – 生化反應 (如：LR、RWC、WUE、量子產率、滲透調節及抗氧化代謝) 等相關定義，藉以提供可量化的田間耐旱性狀評估參考。同時，現已探勘耐旱 QTLs ($qDTY_{1.1/2.2/3.1/12.1}$ 與 $qDTR_8$、$qDLR_{8.1}$、$qLR_{9.1}$ 等)、已選殖耐旱功能基因 (*OsNAC5*、*OsCPK9*、*LEA*、*OsDREB2A*/*2B*、*OsDRAP1*、*OsPYL*/*RCAR5*、*EcNAC67*、*CDPK7*、*CIPK03*/*12*、*WRKY*、*OsITPK2*) 及 miRNA (miR393、miR398、miR160/167、DST-amiRNA 等)，這些成果則已建構分子育種上可操作的遺傳工具。另一方面，育種實務上分子輔助選育/分子輔助回交育種 (MAS/MABC) 與 QTLs 堆疊等策略，已被證實可在多環境背景下，有效提升耐旱的遺傳增益。但現實育種工作上，仍受限於上開 QTLs 區間過大、連鎖累贅及基改作物安全疑慮與基因型 – 環境 (G × E) 交互作用等限制。未來育種及產業應用策略面上，進一步可採高通量表型體分析平臺 (田間多維度偵測器分析平臺) 將核心生理性狀標準化，建立跨環境與

多維度的穩定耐旱選拔指標。同時，利用測序基因分型 (genotyping by sequencing; GBS) 策略，堆疊導入多種不同機制且來自自然種原的耐旱基因型，同步完成重組體之前景、重組及背景的基因型選拔，續進行多區域實驗點與多年期外表型田間試驗，進而建立環境共變量 (environmental covariance) 與實際耐旱反應的 AI 分析模型，得以整合基因型 – 外表型 – 環境 (G × P × E) 可解釋之 AI 與基因組選拔框架，量化單基因與組合效應，及其對產量構成與環境資源分配的貢獻。展望未來，仍需要整合多體學與表型體學 (multi-omics and phenomics integration) 的研究正重新定義植物乾旱適應的理論基礎。透過系統層級資料整合，科學家得以揭示分子調控 – 代謝流 – 生理表型的連續動態過程，並辨識具預測潛力的關鍵代謝節點與調控轉錄因子網絡，並將所得的數據進行有效的整合，方有機會建立作物設計基礎 (crop design based) 的數位育種及智慧管理平臺，以因應未來更形嚴峻之氣候變遷的挑戰。

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Advances in Research on Drought Resistance Mechanisms and Molecular Breeding Strategies in Rice

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Abstract

Lin, D. G., Y. L. Lin, Y. W. Wang, S. Y. Lin, C. B. Li, W. C. Wen, J. Y. Wang, C. S. Wang, and S. Chen. 2026. Advances in research on drought resistance mechanisms and molecular breeding strategies in rice. J. Taiwan Agric. Res. 75(1):51–72.

Rice, a water-demanding staple crop, faces escalating risks from climate change and freshwater scarcity, making improved drought resilience essential for food security and sustainable agriculture. This review synthesizes physiological, biochemical, and molecular responses of rice to drought, emphasizing actionable avenues for breeding. Core adaptive processes include osmotic adjustment, reactive oxygen species (ROS) detoxification, stomatal regulation, and remodeling of root system architecture. Advances from quantitative trait locus (QTL) mapping and gene cloning have identified drought-associated regions and genes- such as the qDTY series (e.g., $qDTY_{1.1}$), $qDTR_{8}$, $qDLR_{8.1}$, and candidate genes including *OsNAC5*, *OsCPK9*, and *LEA* proteins, that provide valuable genetic resources for marker-assisted improvement. Small-RNA regulation constitutes an additional control layer: over 30 drought-responsive microRNAs have been reported, with at least 19 showing defined functions; exemplars include miR393, miR398, miR160, miR167, and DST-amiRNA, which modulate auxin signaling, antioxidative capacity, and stomatal dynamics. On the application front, marker-assisted selection and QTL pyramid have delivered drought-tolerant lines and cultivars. Nevertheless, field expression and precise quantification of drought-related traits remain major bottlenecks that constrain genetic gain. Future progress will hinge on integrating high throughput phenomics with genomic and epigenomic information and contextual environmental data to build multi-level regulatory networks and robust, multidimensional selection indices. Such integrative pipelines are expected to accelerate the development and deployment of drought-resilient rice varieties, advancing the intelligent and sustainable transformation of crop production systems.

Key words: Rice, Drought tolerance, Quantitative trait locus (QTL), Candidate gene, Molecular breeding.

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