生物策略表

類別	生物策略 (Strategy)
生物策略 STRATEGY	腺體排除多餘的鹽分 (Glands remove excess salt)
生物系統 LIVING SYSTEM	海茄苳屬 *Avicennia*
功能類別 FUNCTIONS	#維持體內平衡 #Maintain homeostasis
作用機制標題	有些紅樹林植物的鹽腺利用離子轉運蛋白產生高濃度鈉溶液以排除多餘的鹽分 (The salt glands of some mangrove plants remove excess salt using ion transporters that help create a concentrated sodium solution.)
生物系統/作用機制示意圖	  （海茄苳生態圖：許秋容）

作用機制摘要說明 (SUMMARY OF FUNCTIONING MECHANISMS)

紅樹林通常是灌木 (shrub) 或小喬木 (small tree)，生長在普通植物無法生存的海岸地區。海岸潮汐漲退導致鹽度變化是紅樹林要面對的其中一個逆境。

當紅樹林的根部組織暴露在鹽水時，根部組織中的鹽濃度低於周圍水中的鹽濃度，造成濃度梯度傾向於水中的鹽離子穿過細胞膜進入細胞。然而，紅樹林具有各種耐鹽機制，因物種種類而不同：它們可以隔絕鹽分、累積鹽分或排出鹽分。能隔絕鹽分的植物可以防止鹽分進入根部細胞膜。在含有過多鹽分的植物中，有些會將其累積到較老的葉子中，使鹽分能隨著葉子一起脫落。其它植物則利用葉子上的腺體 (gland) 排出鹽分，排出的鹽水濃度甚至高於海水。

關於鹽分排出的機制已經提出一些假設，通道和幫浦 (channels and pump) 組成的網絡將植物細胞之間的鹽分 （特別是鈉離子），移動到腺體以排出多餘的鹽分。每個植物細胞的細胞質（內部物質）透過細胞膜中的通道連接，使細胞能夠通信、交換資源及轉移過多的鈉離子，最靠近鹽腺的細胞在膜上有特殊的蛋白質，能將鈉離子送到腺體中。首先質子幫浦 (proton pump) (H^+-ATPase) 使用能量傳遞分子 ATP 中的化學能，將質子送入隔室中建立質子濃度梯度。然後，離子交換器（鈉-氫逆向轉運蛋白 sodium-hydrogen antiporter）利用質子梯度的能量往反方向同時傳送鈉離子和質子。質子流向其濃度梯度的過程中，釋放出鈉氫逆向轉運蛋白所需的能量，以將鈉離子傳送到已含高濃

度鈉離子的隔室中。腺體不與細胞接觸的部分被角質層包圍，以防止離子回流到細胞中。鈉離子溶液被濃縮並在鹽腺中形成壓力，然後以濃縮溶液的形式分泌出鹽分。

Mangroves are shrubs or small trees that are found in coastal areas where ordinary plants cannot survive. One difficulty they face in their environment is the different salinity of the tides that come in and out from the coast.

When the mangrove’s root tissues are exposed to salt water, the concentration of salt in the vessels of the root is lower than the concentration of salt in the water surrounding the plant. This concentration gradient would tend to drive salt ions across the plant tissue’s membranes into its cells. However, mangroves have various salt tolerance mechanisms that vary with species: they can exclude salt, accumulate salt, and/or excrete salt. Plants that exclude salt prevent it from entering the membranes of their roots. In other plants that do end up containing excess salt, some accumulate it into older leaves so it can be shed with the leaves. Others excrete salt, in much higher concentration than seawater, through glands on their leaves.

Research on the mechanism of salt excretion has led to the hypothesis that a network of channels and pumps moves salt (specifically, sodium ions) between plant cells to the glands that eventually excrete the excess salt. The cytoplasm (inner material) of each plant cell is connected by channels in the cell membranes, enabling cells to communicate, exchange resources, and transfer excess sodium ions. The membranes of the cells closest to the salt glands contain specialized proteins that pump sodium from the cell into the gland. First, proton pumps (H^+-ATPases) use chemical energy from the energy-transporting molecule ATP to drive protons into a compartment and establish a proton concentration gradient. Then an ion exchanger, the sodium-hydrogen antiporter, uses the energy of the proton gradient to move sodium ions and protons in opposite directions, at the same time. The process of protons flowing down their concentration gradient releases energy needed by the sodium-hydrogen antiporter to move sodium ions to a compartment already high in sodium. Parts of the gland that aren’t in contact with the cell are surrounded by a cuticle that prevents ions from flowing back into the cells. The sodium solution becomes concentrated and builds up pressure in the salt gland, which then secretes the salt as a concentrated solution.

文獻引用 (REFERENCES)

[關於一般的鹽腺 (salt gland)] 對於多葉米草 (*Spartina foliosa*) (Levering and Thomson, 1971) 及無葉檉柳 (*Tamarix aphylla*) (Thomson et al., 1969) 鹽腺微構造的前人研究顯示鹽腺周圍具有角質層，在葉肉組織與外界環境之間形成了一道厚厚的屏障。鹽草 (*Distichlis spicata*) 中的新發現顯示這些離子通過鹽腺底部沒有角質層包覆的穿透區域，被運送到鹽腺中，而角質層能阻止離子回流 (backflowing) 到葉肉組織中 (Semenova et al., 2010)。鹽腺中累積的離子，通過底部穿透區域及原生質絲

(plasmodesmata) 因角質層存在而產生的流體壓力，從鹽腺的孔洞分泌出來。」(Yuan et al. 2016: 6)

「在所有多細胞鹽腺中 (Thomson, 1975; Thomson et al., 1988)，角質層 (cuticle) 會從底部的細胞 (the basal cell) 沿著腺體的側面向外延長包圍著鹽腺。」(Dschida et al. 1992: 504)

「…我們認為離子在腺體間以共質體途徑（通過細胞原生質及通道）被吸收及運輸，然後從共質體 (symplast)（細胞膜下方的區域）釋放到腺體外部，隨後在葉片表面累積鹽分分泌。另外，從質外體 (apoplast)（細胞壁內的範圍）到共質體的初期吸收需要消耗能量，牽涉到細胞原生質膜的 H^+/ATP 酶（質子幫浦）及電子化學質子梯度的建立。電子化學質子梯度是由正離子載體及/或通道所利用作吸收離子。離子通過共質體移動到腺體的分泌細胞，可能是透過擴散作用及細胞與細胞之間的原生質絲 (plasmodesmata)（連接通道）(Fitzgerald and Allaway 1991)。離子從分泌細胞往外的釋放亦可能牽涉到與電子化學質子梯度類似的建立，促使正離子載體及/或通道作用。我們發現這個模型與根部離子運輸的假說有很多相似之處 (Hanson 1978; Clarkson 1991)，在構造上或生理上的證據都有著高度相似性。」(Balsamo et al. 1995: 667)

“[Regarding salt glands in general] previous studies on the salt gland ultrastructure in *Spartina foliosa* (Levering and Thomson, 1971) and *Tamarix aphylla* (Thomson et al., 1969) demonstrated that cuticles were present around the salt glands, and they formed a thick barrier from the mesophyll and the external environment. New findings of *Distichlis spicata* showed that these ions were transported into the salt gland through the bottom penetration area that was not covered by the cuticles of the salt gland, and the cuticles can prevent the ions from backflowing into the mesophyll (Semenova et al., 2010). Ions accumulated in the salt gland via the bottom penetration area and plasmodesmata generated fluid pressure due to the presence of the cuticle, and then secreted through salt gland pores.” (Yuan et al. 2016: 6)

“As with all multicellular salt glands (Thomson, 1975; Thomson et al., 1988), the cuticle encloses the glands, extending outward from the basal cell along the sides of the glands. ” (Dschida et al. 1992: 504)

“...we suggest that ions are taken up [and] transported symplastically [through cell cytoplasm and channels] through the glands, and released from the symplast [area beneath the plasma membrane] to the exterior of the glands with the subsequent appearance and accumulation of salt secretions on the surface of the leaves. Also, the initial uptake into the symplast from the leaf apoplast [area within cell walls] is energy dependent, involving the H^+/ATPase [proton pump] in the plasma membrane of the cells with the establishment of an electrochemical proton gradient. This electrochemical proton gradient is utilized by cation carriers and/or channels for uptake. Ion movement through the symplast to the secretory cells of the glands is probably diffusive and cell to cell via plasmodesmata [connecting channels] (Fitzgerald and Allaway 1991). Outward release of the ions from the secretory cells also probably involves the similar establishment of an electrochemical proton gradient that drives the action of cation carriers and/or channels. We note that this model has many similarities to hypothesis of ion transport across roots (Hanson 1978; Clarkson 1991), and there are strong similarities in the evidential bases for these, both structurally and physiologically." (Balsamo et al. 1995: 667)

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延伸閱讀

生物系統延伸資訊連結 (LEARN MORE ABOUT THE LIVING SYSTEM/S)

https://en.wikipedia.org/wiki/Avicennia

撰寫/翻譯/編修者與日期

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