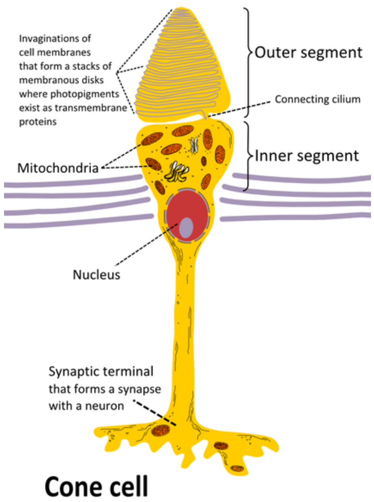
生物策略表

類別	生物策略 (Strategy)
生物策略 STRATEGY	感光蛋白主導避開陰影處生長的行為 (Photoreceptor proteins direct shade avoidance behavior)
生物系統 LIVING SYSTEM	阿拉伯芥 *Arabidopsis thaliana* (Thale cress)
功能類別 FUNCTIONS	#適應表現型 #對訊號反應 #從環境感應光（非可見光譜） #從環境感應光（可見光譜） #轉導/轉換訊號 #Adapt phenotype #Respond to signals #Sense light (non-visible spectrum) from the environment #Sense light (visible spectrum) from the environment #Transduce/convert signals
作用機制標題	阿拉伯芥植株通過偵測與陰影相關的紅色和藍色光波長變化來最大化光合作用活動，促使引導植物直接遠離陰影生長的蛋白質合成 (Thale cress plants maximize photosynthetic activity by detecting changes in wavelengths of red and blue light associated with shade, triggering protein production to direct growth away from shaded areas.)
生物系統/作用機制示意圖	 

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

植物經常生長在各類植物群聚稠密的環境中，在這種環境中能獲取陽光是一件奢侈的事情。為了最大化光合作用的機會，植物已經演化出複雜的生化感應途徑來啟動避蔭綜合症狀 (shade avoidance syndrome, SAS)。SAS 會使植物往遠離陰影的地方生長，這對維持植物的競爭優勢相當重要。阿拉伯芥則演化出雙重而繁冗 (redundant) 的感應機制來遠離陰影。光敏素 B (phytochrome B, phyB) SAS 途徑取決於偵測紅光與遠紅光 (R:FR) 比例的降低。生長於阿拉伯芥上方頂層的植物，其葉綠素會吸收紅光，且胞壁散射遠紅光。因此，R/FR 比例的降低（植株曝露於較少紅光）對處於冠層陰影中的阿拉伯芥來說是一個很好的訊號，它應該開始進行 SAS 過程以「逃離」陰影。當阿拉伯芥的葉片吸收更多遠紅光時，光敏色素分子 (phytochrome molecule) 會改變形狀，導致一系列反應產

生使植物遠離陰影生長的相關蛋白質。也有一個平行系統是由藍光的減少所觸發。相互競爭光線的植物其葉綠素會大量吸收藍光，因此藍光的減少是陽光被阻擋的可靠指標。

Plants often grow in densely populated environments in which access to sunlight is a precious commodity. In order to maximize opportunities for photosynthesis, plants have evolved complex biochemical sensory pathways that initiate shade avoidance syndrome (SAS). SAS results in growth away from shade and is of critical importance to maintaining a plant's competitive edge. The thale cress has evolved dual, redundant sensory mechanisms for avoiding shade. The phyB (phytochrome B) SAS pathway depends on detecting a decrease in the ratio of red light to far-red light (R:FR). In plants growing in the canopy above a thale cress, chlorophyll absorbs red light and cell walls scatter far-red light. Thus, a decrease in the R:FR ratio (the plant is exposed to less red light) is a good signal for the thale that it is in the shade of the canopy and should begin SAS processes to "escape". When thale cress leaves absorb more far-red light, the phytochrome molecule changes shape leading to a cascade of reactions that produce proteins related to growth away from the shade. A parallel system is triggered by a reduction in blue light. Chlorophyll from competing plants strongly absorbs blue light, so a reduction in blue light is a reliable indication that sunlight is being blocked.

文獻引用 (REFERENCES)

「形態可塑性 (morphological plasticity) 的一個主要例子即是 SAS。SAS 反應通常包括莖和葉柄的延長 (elongation)、葉片下偏生長 (hyponasty)、分枝減少，以及植株幼芽的向光性轉往樹冠間隙方向…這些訊號的最佳特徵是紅光/遠紅光比例 (R:FR; 660–670/725–735 nm)，而該比例降低是由於樹冠層中的葉綠素大量吸收紅光、細胞壁和其他植物的組成散射(scatter) 遠紅光光子所致。」(Keller et al.2011: 195-6)

「光敏素 B (phyB) 是感應 R:FR 比例降低的主要光感受器 (photoreceptor)，亦控制 SAS 表現型的初始外觀…SAS 對於低 R:FR 比例的反應（葉柄延長及葉片下偏生長）取決於透過阿拉伯芥色胺酸胺基轉移酶 1 (TAA1) 路徑的生長素生合成增加，以及透過生長素運輸蛋白 (the auxin efflux carrier) PIN3 的極性生長素運輸。徒長素 (gibberellin, GA) 的生產增加，或許是生長素增加造成的反應，也是低 R:FR 會使葉柄延長反應表現的原因之一…徒長素生產增加會觸發 DELLA 蛋白被 26S 蛋白酶體 (26S proteasome) 分解，DELLA 蛋白是一群會過度抑制生長的五種核蛋白。DELLA 蛋白會與光敏素互動因子 (PIFs) 結合並將其去活化，這些是在低 R:FR 下啟動 SAS 反應中參與的生長促進轉錄因子…植物能它對藍光的衰減表現出強烈的 SAS 類似反應…藍光反應需要 cry1，並由荷爾蒙所調節，它與反應於低 R:FR 比例而削弱 (depletion) phyB Pfr 所活化的路徑只有有限的重疊…PIF4 及 PIF5，是鹼性/螺旋-環-螺旋 (bHLH) 轉錄因子，已知能調控 phyB 去活性造成的形態反應，這亦參與了藍光減弱所啟動的 SAS 表現型反應。」(Keller et al. 2011: 196)

「阿拉伯芥的蓮座形植株 (rosette) 能對藍光減弱表現出非常明顯的 SAS 反應，包括顯著的葉片下偏生長和 L:P 比例的降低…這種反應主要由 cry1 調控…本研究中描述的兩種 SAS 反應（葉片下偏生長和葉片形態改變），儘管是反應於競爭訊號（低 R:FR 或低藍光）而同時表現，但似乎是被不同的機制所調控。」(Keller et al。2011: 200)

「然而 DELLA 降解作用似乎對於調節幼苗及蓮座形植株因低 R:FR 比例而產生的 SAS 反應發揮了重要作用，它並非被藍光減少所活化，而且不直接參與 SAS 反應的產生。」(Keller et al. 2011：201)

「PIF4 和 PIF5 都有存在的必要，才能完全表現因藍光減少而產生的下偏生長反應…沒有證據證明 cry 會誘導 PIF 的降解作用、或是 cry 與 PIF 之間有物理上的交互作用存在…因藍光減少活化 PIF4 和 PIF5 而產生的潛在機制可能牽涉 bHLH 相關因子－HFR1 的參與…訊息溝通理論 (communication theory) 認為在嘈雜環境中進行可靠傳輸和處理訊息，冗餘 (redundancy) 是必要的條件。」(Keller et al. 2011: 203)

「植物使用低 R:FR 比例和低藍光作為競爭對手靠近時的部分冗餘訊號…phyB 和 cry1 分別感應的訊號也活化了個別的訊號網絡，這些訊號網絡對於所牽涉的分子參與者只展現了有限的重疊。平行控制途徑頻繁地匯聚在主要的調控節點中…PIF4 和 PIF5 是核心 SAS 途徑的關鍵中心，它整合了來自控制植物樹冠之中適應可塑性的主要光訊號路徑之訊息。」(Keller et al. 2011: 204)

“A prime example of morphological plasticity is the shade avoidance syndrome (SAS). SAS responses typically include increased elongation of the stem and petioles, leaf hyponasty, reduced branching and phototropic orientation of the plant shoot towards gaps in the canopy...The best characterized of these signals is the red/far red ratio (R:FR; 660–670/725–735 nm), which decreases in response to canopy density because of the strong absorption of red light by chlorophyll and scattering of far-red photons by cell walls and other plant constituents.” (Keller et al. 2011: 195-6)

“Phytochrome B (phyB) is the major photoreceptor that senses a reduction in the R:FR ratio, and controls the initial appearance of SAS phenotypes...SAS responses to low R:FR (increased petiole elongation and leaf hyponasty) depend on increased auxin biosynthesis through the TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1) pathway, and polar auxin transport by the auxin efflux carrier PIN3. Increased gibberellin (GA) production, perhaps in response to increased auxin, is also required for the expression of petiole elongation responses to low R: FR... Increased GA production triggers degradation by the 26S proteasome of DELLA proteins, a group of five nuclear proteins that redundantly repress growth. DELLA proteins bind to and inactivate PHYTOCHROME INTERACTING FACTORS (PIFs), which are growth-promoting transcription factors involved in the elicitation of SAS responses to low R:FR...plants can present strong SAS-like responses to blue light attenuation...blue light responses required cry1, and were mediated through hormonal pathways that showed only limited overlap with the pathways activated in response to phyB Pfr depletion by low R:FR ratios...PIF4 and PIF5, which are basic/helix-loop-helix (bHLH) transcription factors known to mediate morphological responses to phyB inactivation, are also required for the elicitation of the SAS phenotype in response to blue light attenuation." (Keller et al. 2011: 196)

"*Arabidopsis* rosettes can display very marked SAS responses to blue light attenuation, including pronounced hyponasty and a reduced L: P ratio... this response is predominantly mediated by cry1...The two SAS responses characterized in this study (hyponasty and altered leaf morphology), although concomitantly displayed in response to competition signals (low R:FR or low blue light), appeared to be controlled by different mechanisms." (Keller et al. 2011: 200)

"[W]hereas DELLA degradation appears to play a significant role in mediating SAS responses to low R:FR ratios in seedlings and rosette plants, it was not activated by blue light attenuation, and not directly involved in the production of the SAS response." (Keller et al. 2011: 201)

"[B]oth PIF4 and PIF5 need to be present for full expression of the hyponastic response to blue light attenuation... There is no evidence of cry-induced degradation of PIFs, or of physical interactions between crys and PIFs...A potential mechanism whereby blue light attenuation activates PIF4 and PIF5 might involve a related bHLH factor, HFR1...Communication theory maintains that redundancy is a requirement for the reliable transmission and processing of information in noisy environments." (Keller et al. 2011: 203)

"[P]lants use low R:FR and blue light as partially redundant signals of the proximity of competitors... signals, perceived by phyB and cry1, respectively, also activate separate signaling networks that show limited overlap with regard to the molecular players involved. Parallel control pathways frequently converge in major regulatory nodes... PIF4 and PIF5 are critical hubs in the core SAS pathway, which integrate information from the principal light signaling routes that control adaptive plasticity in plant canopies." (Keller et al. 2011: 204)

參考文獻清單與連結 (REFERENCE LIST)

Keller, M. M., Y. Jaillais, U. V. Pedmale, J. E. Moreno, J. Chory, and C. L. Ballaré. (2011). Cryptochrome 1 and phytochrome B control shade-avoidance responses in *Arabidopsis* via partially independent hormonal cascades. *The Plant Journal* 67: 195-207. (https://doi.org/10.1111/j.1365-313X.2011.04598.x)

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/Arabidopsis_thaliana
撰寫/翻譯/編修者與日期
顏子傑翻譯 (2018/10/29)；譚國鋈編修 (2021/03/31)；許秋容編修 (2021/05/17)
AskNature 原文連結
https://asknature.org/strategy/photoreceptor-proteins-direct-shade-avoidance-behavior/#.W9ajstUzaUl