生物策略表

類別	生物策略 (Strategy)
生物策略 STRATEGY	葉子形狀使陽光吸收最佳化 (Leaf shapes optimize sunlight)
生物系統 LIVING SYSTEM	橄欖樹 *Olea europaea* (Olive trees)
功能類別 FUNCTIONS	#適應外表型 #獲取、吸收、或過濾能量 #分配能量 #改變大小/形狀/質量/體積 #Adapt phenotype #Capture, absorb, or filter energy #Distribute energy #Modify size/shape/mass/volume
作用機制標題	橄欖樹透過的特化形狀及適應性的葉片應對不斷變化的環境條件，使陽光吸收最佳化 (Leaves of olive trees optimize sunlight harvesting by differing in shape and being flexible to changing conditions)
生物系統/作用機制示意圖	

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

在一些落葉樹種中，樹冠外部的葉子與樹冠內部的葉子有所不同。外部的葉子被稱為「陽性葉」，而內部的葉子被稱為「陰性葉」。這些葉子在形狀、內部解剖構造和化學上都有差異，這些差異轉化為有效利用各種太陽輻射的專門能力。

陽性葉通常比陰性葉更小、更細長且更厚，具有更多層含葉綠素的組織和更大範圍的內部維管束系統。一般認為陽性葉在獲取和使用直接的太陽輻射方面有更佳的適應能力（以太陽輻射的強度不至於引起過熱和其他與逆境相關的損害為前提）。它們細長的形狀跟照射到樹冠內部陰性葉的較高的太陽輻射有關。陰性葉似乎能有效利用散射的太陽光，該輻射是來自直射光被其它物體（如外部陽性葉片）散射後而到達樹冠內層。陰性葉也存在背對盛行陽光照射側的外部樹冠層。

看來外部的陽性葉片特性會隨環境條件而改變（表現出可塑性），並且它們獨特的形狀會影響陰性葉所處的樹冠內部環境。陽性葉的可塑性可能有助於穩定內部冠層狀況，從而緩解非生物的壓力。遺傳變異和樹木大小也會影響葉片的特性，但透過陽性和陰性葉片對環境的不同反應，可以使整棵樹的光合作用達最佳化。陽性和陰性葉也出現在其他物種中。橡樹的外部葉片有著較窄的裂片，而陰性葉片的裂片則較寬。

In some deciduous trees, the leaves on the exterior of the tree canopy differ from those inside the tree canopy. The exterior leaves are referred to as “sun leaves,” while the interior leaves are “shade leaves.” These leaves have differences in shape, internal anatomy, and chemistry that translate into specialized abilities to use different kinds of solar radiation effectively.

Sun leaves are typically smaller, more elongate, and thicker than shade leaves, with more layers of chlorophyll-containing tissues and more extensive internal vascular systems. It is thought that sun leaves are better adapted to capture and use direct solar radiation (when it isn’t too intense to cause heat and other stress-related damage). Their elongate shape is also correlated with higher levels of solar radiation reaching the inner canopy where the shade leaves are located. Shade leaves appear to effectively use diffuse solar radiation, which reaches the inner canopy after having been scattered by other objects, like the outer sun leaves, in the path of direct light. Shade leaves can also be found on the exterior canopy on the side that faces away from the prevailing sun.

It appears that exterior sun leaf characteristics can change with environmental conditions (they show plasticity), and that their shape in particular can influence the internal canopy environment that shade leaves experience. Plasticity in sun leaves seems to help stabilize inner canopy conditions, buffering it from abiotic stresses. Genetic variation and tree size also affect leaf characteristics, but it seems that whole-tree photosynthesis can be optimized by having sun and shade leaves respond differently to the environment. Sun and shade leaves occur in other species, too. In oaks, external leaves have narrower lobes while the lobes of shade leaves are broader.

文獻引用 (REFERENCES)

「1. 冠層可塑性，同一個體樹冠內不同葉片表現型具有複雜的功能性和演化上的意義，有待進一步評估。我們假設這可能導致冠層不同位置的葉片隨著異速生長 (allometric growth) 和族群遺傳結構變化造成差異。

2. 利用八個形態和生理特徵估算內冠層和外冠層的葉片外表型…利用這些數據，我們研究了葉片外表型隨植物大小、遺傳過程，以及在對冠層內外環境條件的反應而變化的程度。

3. 在野外測量的樹木大小顯然與陽性葉的外表型有關，但與陰性葉的外表型無關。陽性葉的外表型取決於直射光和散射光，而陰性葉的外表型只與散射輻射相關。另外，樹冠層內部的光照程度會受外部葉片的形狀影響，增加長度的陽性葉可以使用內部樹冠層接受到較高的輻射。

4. 冠層內部葉片和外部葉片的野外外表型與族群間的遺傳變異相關。相反地，在移地栽種試驗中 (在一般花園中)，不同的基因型表現出同質的陽性外表型，而族群之間的表型差異在陰性葉則仍然明顯。

5. 我們的結論與我們的研究假說相符，樹冠層可塑性既是植物面對環境的原因，也是結果，並且可能導致葉片間遺傳多形性的表達差異。再者，我們認為它可以有助於緩解非生物壓力，並有助於樹冠內光利用的分配。」(de Casas et al. 2011: 802)

「在冠層不同位置模組的不同表型可能會使整體性能最大化，在光線獲取條件最佳的情況下（即在春季和夏季在無乾旱的情況下的清晨和較晚的下午）陽性葉最活躍 (Diaz-Espejo， Nicolas＆Fernandez 2007)；而陰性葉確保了全年穩定的光合作用。」(de Casas et al. 2011: 810)

“1. Canopy plasticity, the expression of different leaf phenotypes within the crown of an individual tree has complex functional and evolutionary implications that remain to be thoroughly assessed. We hypothesized that it can lead to disparity in how leaves in different positions of the canopy change with allometric growth and population genetic structure.

2. Leaf phenotypes of the inner and outer canopy were estimated using eight morphological and physiological characters…With these data, we investigated the extent to which leaf phenotypes change with plant size, genetic processes and in response to environmental conditions inside and outside the canopy.

3. The size of trees measured in the field was clearly associated with the phenotype of sun [leaves] but not to that of shade leaves. The phenotype of sun leaves depended on both direct and diffuse light, while that of shade leaves was found to correlate only with diffuse radiation. Additionally, light availability inside the canopy was conditioned by the shape of external leaves, and increasing elongation of sun leaves led to higher radiation in the inner canopy.

4. The field phenotypes of both inner and outer canopy leaves were correlated with genetic variation among populations. Conversely, in the common garden, the different genotypes expressed a homogeneous sun phenotype, while phenotypic differences among populations remained apparent in shade leaves.

5. We conclude that, in agreement with our working hypothesis, canopy plasticity is both cause and consequence of the environment experienced by the plant and might lead to the differential expression of genetic polymorphisms among leaves. Furthermore, we propose that it can contribute to buffer abiotic stress and to the partition of light use within the tree crown.” (de Casas et al. 2011: 802)

“The diverging phenotypes of modules in different positions of the canopy might thus maximize overall performance, with sun leaves most active when conditions for light capture are optimal (i.e. during spring, and early morning and late afternoon in summer without drought (Diaz-Espejo, Nicolas & Fernandez 2007) and shade leaves ensuring a stable photosynthetic performance throughout the year.” (de Casas et al. 2011: 810)
參考文獻清單與連結 (REFERENCE LIST)
de Casas, R. R., P. Vargas, E. Pérez-Corona, E. Manrique, C. García-Verdugo, and L. Balaguer. (2011). Sun and shade leaves of *Olea europaea* respond differently to plant size, light availability and genetic variation. *Functional Ecology* 25: 802-812. (https://doi.org/10.1111/j.1365-2435.2011.01851.x) National Evolutionary Synthesis Center (NESCent). (March 31, 2011). It's good to have a shady side: sun and shade leaves play different roles in tree canopies. *EurekAlert!* Retrieved from: https://www.eurekalert.org/pub_releases/2011-03/nesc-igt033111.php Vogel, S. (2009). Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist* 183: 13-26. (https://doi.org/10.1111/j.1469-8137.2009.02854.x) Sack, L., P. J. Melcher, W. H. Liu, E. Middleton, and T. Pardee. (2008). How strong is intracanopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* 93:829-839. (https://doi.org/10.3732/ajb.93.6.829) Burns, K. C. and Sam Beaumont. (2009). Scale-dependent trait correlations in a temperate tree community. *Austral Ecology* 34: 670-677. (https://doi.org/10.1111/j.1442-9993.2009.01973.x)
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生物系統延伸資訊連結 (LEARN MORE ABOUT THE LIVING SYSTEM/S)
https://en.wikipedia.org/wiki/Olea_europaea
撰寫/翻譯/編修者與日期
蔡心云翻譯 (2020/03/31)；譚國鋈編修 (2020/06/01)；許秋容編修 (2020/06/05)
AskNature 原文連結
https://asknature.org/strategy/leaf-shapes-optimize-sunlight/