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# A brief review on leaf anatomy of plants with certain peculiar modes of photosynthesis

Uma breve revisão sobre a anatomia foliar de plantas com determinados modos peculiares de fotossíntese

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## ABSTRACT

*(Leaf anatomy of plants with certain peculiar modes of photosynthesis). The majority of the terrestrial plants are C<sub>3</sub> and present leaves with the mesophyll divided into palisade and/or spongy mesophyll. However, some plants present specific patterns of leaf anatomy related to peculiar photosynthetic responses, such as the C<sub>4</sub> and CAM cycles and adaptations to dry, hot environments. A review on the data of leaf anatomy of C<sub>4</sub> and CAM plants is presented as well as plants presenting scleromorphic leaves and plants with amphistomatous leaves related to the photosynthetic responses usually observed in these groups.*

**KEY WORDS:** *kranz anatomy, amphistomy, photosynthesis, scleromorphism, succulence.*

## RESUMO

*Anatomia foliar de plantas com modos peculiares de fotossíntese. A maioria das plantas terrestres é C<sub>3</sub> e apresenta folhas com uma estrutura anatômica geral de mesófilo composto de parênquima paliçádico e/ou esponjoso. Entretanto, algumas folhas apresentam padrões de anatomia foliar relacionadas a tipos fotossintéticos peculiares, como os ciclos C<sub>4</sub> e CAM, ou adaptações a ambientes secos e quentes. É apresentada uma revisão de dados sobre anatomia foliar de plantas C<sub>4</sub>, CAM, escleromorfas e anfiestomáticas relacionados aos perfis fotossintéticos comumente observados nesses grupos.*

**PALAVRAS-CHAVE:** *anatomia Kranz, anfiestomia, fotossíntese, escleromorfismo, succulência.*

## I. Introduction

The majority of terrestrial plants carry out the C<sub>3</sub> photosynthesis (SAGE; MCKOWN, 2006). Although these plants present a large variability of photosynthetic responses regarding optimal temperature, carbon assimilation rate, tolerance to drought etc., the foliar anatomical structure follows a general pattern: stomata in the abaxial surface of the epidermis and mesophyll with palisade and spongy chlorenchyma in the dicotyledons and only spongy chlorenchyma in the monocotyledons (ESAU, 1984).

Variations on this pattern are found in the C<sub>3</sub> plants. However, some peculiar photosynthetic pathways, such as C<sub>4</sub> and CAM, as well as some specific environmental conditions, such as those found in dry tropical ecosystems, are related to singular patterns of leaf anatomy (GUARALNICK et al. 2002). Both ways are in fact derived from the C<sub>3</sub>-pathway, which means, C<sub>4</sub> and CAM presents biochemical steps before the CO<sub>2</sub> enters in the C<sub>3</sub> cycle (EHLERINGER; MONSON, 1993). The aim of this study is to review the relationships between these peculiar patterns of leaf anatomy and the related photosynthetic responses.

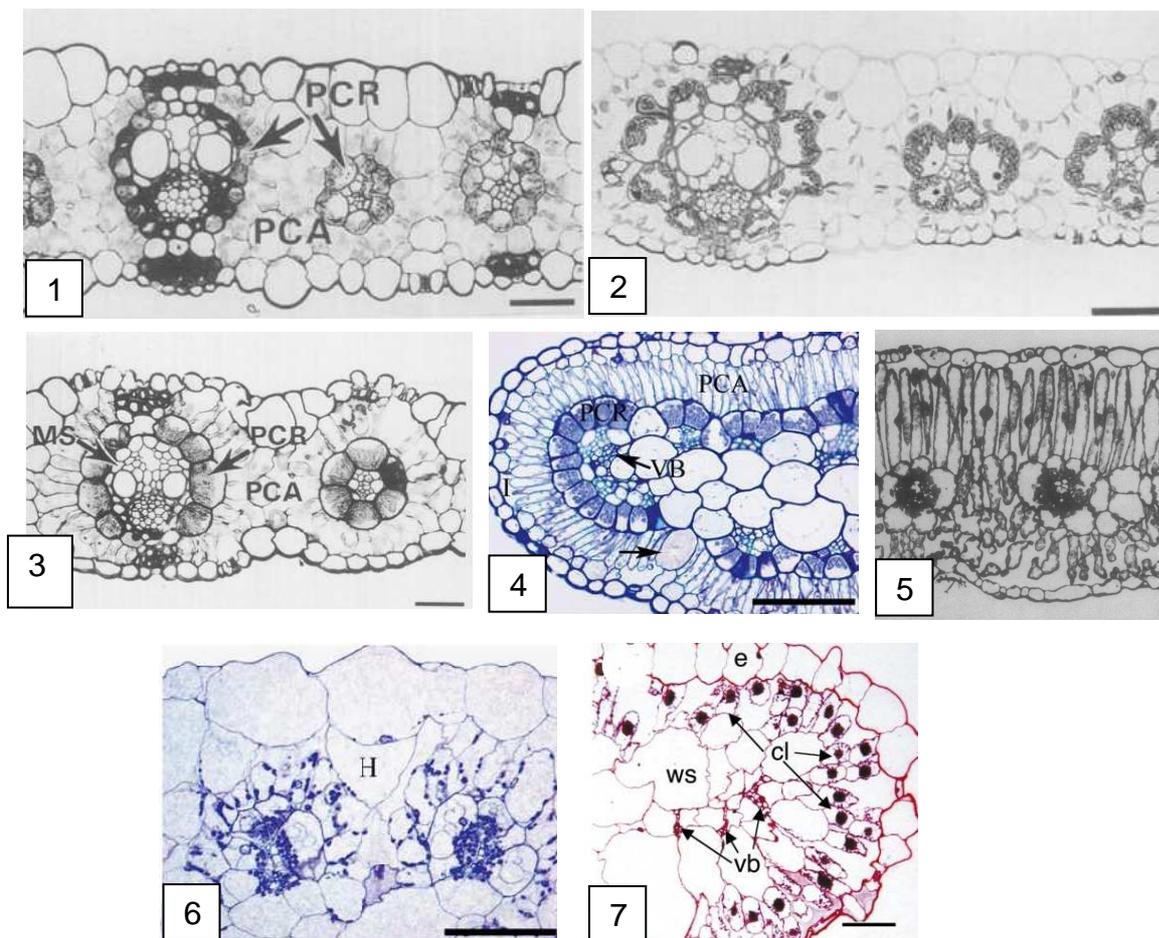
## II. Methods

This minireview was mainly based on google scholar. The articles were searched by crossing the words C<sub>4</sub>, CAM, amphistomy (amphistomatous), scleromorphic leaf, photosynthesis. The studies that related optical anatomical features (ultrastructural data were not considered) with photosynthetic responses were selected. As the amount of articles was of more than 500 texts, a convenience sample was taken, with special regard to the review articles, the ones with atypical findings and the references of the selected texts.

## Leaf anatomy of C4 plants

The relationship between structure and function, a classic paradigm of Biology, is clearly illustrated in the relationship between Kranz anatomy and C4 photosynthesis. Kranz anatomy is defined as that where the leaf blade presents the nerves surrounded by two layers of chlorenchyma: the inner one is the vascular (or Kranz) sheath and the outer is the mesophyll (ESAU, 1984; CUTTER, 1987). C4 photosynthesis is defined as that where there is a spatial separation of the biochemical paths: the mesophyll assimilates the atmospheric CO<sub>2</sub> through the phosphoenolpyruvate-carboxylase (PEPcase), producing organic acids that are transferred to the vascular sheath, where the carbon will be released by the action of decarboxylases and incorporated in carbohydrates through the C<sub>3</sub> cycle via Rubisco. As a consequence, the loss of carbon through photorespiration in C4 plants is not detectable, although such a metabolic cycle is active in most of the C4 species studied. (LANGE et al. 1982; MAJEROWICZ, 2004)

Among the monocotyledons, C4 species are present in only three families: Poaceae, Cyperaceae and Hydrocharitaceae. Among the eudicotyledons, 16 families were identified as having C4 species (EDWARDS et al., 2004). Almost all C4 plants are shrubs or herbs; only some species present as small (up to 8 m) trees (PEARCY; TROUGHTON, 1975). So, anatomical structure of the leaves of C4 plants is also related to the taxonomic group to which the species belong: C4 grasses (Figures 1-3) and sedges present all the mesophyll in contact with the Kranz sheath (EAMES, 1925; ESAU, 1984; MAUSETH, 1988), with a system of small longitudinal veins denser than their related C<sub>3</sub> plants (UENO et al., 2006). The anatomical structure of the C4 eudicotyledons is more diversified (figures 4-7), with at least five patterns of organization and commonly presenting layers of palisade and spongy mesophyll not in contact with the Kranz sheath (EDWARDS; FRANCESCHI; VOZNESENSKAYA, 2004; FANK-DE-CARVALHO; GRACIANO-RIBEIRO, 2005; MUHAIDAT; SAGE; DENGLER, 2007).



## Legends of the figures

Figures 1-7. Main basic aspects of leaf anatomy of C4 plants. 1-3. Poaceae C4 leaves (Dengler et al. 1994). 1. *Panicum bulbosum*, a typical NADP-ME. 2. *Melinis minutiflora*, a typical PCK C4. 3. *Eragrostis dielsii*, a

typical NAD-ME. 4-7. Dicotyledonous leaves. 4. (MUHAIDAT; SAGE; DENGLER, 2007). *Kochia scoparia* (Asteraceae), a full C4 plant. 5. (MOORE et al., 1987). *Parthenium hysterophorus* (Asteraceae), an intermediate C3-C4, with a high, but not complete, degree of Kranz organisation. 6. (MUHAIDAT; SAGE; DENGLER, 2007). *Portulaca grandiflora* (Portulacaceae), an intermediate C4-CAM. C4 metabolism occurs in the mesophyll. In the water storage tissue (H), there is nocturnal accumulation of organic acids. 7. (Voznesenskaya et al. 2002). *Bienertia cycloptera* (Amaranthaceae), a C4 plant without Kranz anatomy. PCR = Kranz sheath. PCA = mesophyll. MS = mestome sheath. VB = vascular bundle. e = epidermis. Ws = water storage tissue. Cl = chloroplasts.

Almost all C4 plants present the Kranz anatomy. An exception is made in *Borszezowia aralocaspica* and *Bienertia cycloptera* (Figure 7), dicotyledons from the family Amaranthaceae (or Chenopodiaceae according to the taxonomist), and in the species from the family Hydrocharitaceae (that are of an underwater cycle of life), where the C4 pathway occurs in each one of the cells of the mesophyll, that are large, with a spherical central cytoplasm full of mitochondria and chloroplast, and linked to the extremities through cytoplasmic channels (SAGE, 2002; VOZNESENSKAYA et al. 2002; EDWARDS; FRANCESCHI; VOZNESENSKAYA, 2004).

Notwithstanding, many plants present Kranz anatomy but are actually C3 (KANAI; KASHIWAGI, 1975). Which means, in the case of the relationship between Kranz anatomy and C4 metabolism, the structure precedes the function: the structure is necessary, but not sufficient, for the establishment of the C4 metabolism. The C4 metabolism is established at the moment where there is a spatial dissociation in the photosynthetic enzymes: Pcpase acting in the mesophyll and Rubisco acting in the vascular sheath. (LANGE et al., 1982; ANTONIELLI et al., 2002)

However, reflecting the small gradual changes that living beings pass through during the evolutionary process, there are gradations in the Kranz anatomy and also functional gradations in the C4 pathway. At the present, the functional gradations of the C4 plants are: the complete C4, the C4-like, the C3-C4 intermediate and the C4-CAM intermediate (KU et al., 1991).

The complete C4 plants present high carbon assimilation rates, no inhibition by the atmospheric O<sub>2</sub> and photosynthetic compensation point of CO<sub>2</sub> inferior to 10 ppm. Histochemical studies in anatomical slices show that these plants present a complete spatial dissociation of the C4 enzymes: practically no Rubisco in the mesophyll but all the Rubisco in the vascular sheath (KU et al. 1991).

The C4-like plants are partially inhibited by higher concentrations of atmospheric O<sub>2</sub>. Histochemical studies reveal that most species present the Rubisco both in the mesophyll and the vascular sheath, but some species present a full dissociation of this enzyme, indicating that other regulatory processes, still not very well understood, may interfere with the complete expression of the C4 characteristics (KU; EDWARDS, 1980).

The C3-C4 intermediates are a heterogeneous group, presenting many degrees of the organization of the Kranz anatomy and photosynthetic profiles with just some of the characteristics of the C4 plants. For example, some intermediates may present just a sketchy Kranz sheath, with fewer cells than the C4 plants, or an inner sheath with open extremities, or also (Figure 5) the mesophyll not in full contact to the sheath (BROWN; HATTERSLEY, 1989). Some other intermediates behave as C3 if exposed to low temperatures (KU et al. 1983; MONSON; SCHUSTER; KU, 1987; SUDDERTH et al., 2007), while others can express a C3 feature if they grow submerged in water or a C4 feature if growing terrestrially (UENO, 1998). Also, some plants with green stems and petioles may have leaf blades of C3 metabolism at the same time the vascular bundles of the stem and petioles can fix carbon via malate decarboxylase, which characterizes a C4 pathway. In such plants, malate comes either from the surrounding cells of the vascular bundles or from the roots that eventually are able to absorb sugars and bicarbonate, providing carbon via xylem (HIBBERD; QUICK, 2002).

Some C4-CAM intermediates were identified in the Portulacaceae family (Figure 6), with some peculiarities in the leaf anatomy: the presence of Kranz anatomy and a well developed water storage parenchyma (GUARALNICK et al., 2002). In such species, the C4 metabolism occurs in the mesophyll while the region of the aquiferous parenchyma accumulates organic acids during the nocturnal period, characterizing the CAM metabolism (SAGE, 2002).

Obviously, the photosynthetic responses and the leaf anatomy of C4 plants are not fully expressed in shaded leaves, meaning that leaves which for any reason had not received enough light in intensity and/or duration during their development (SAGE; MCKOWN, 2006). Also experimental stressful conditions, such as salinity, luminosity, temperature, nutrient availability alter the morpho-physiological expression of the leaves (SAM et al. 2003).

The C4 metabolism may be subdivided into three categories, according to the type and position, in the Kranz sheath, of the decarboxylase: NADP-ME (malic desidrogenase dependent of adenine nicotinamide dinucleotide phosphate), enzyme located in the chloroplast; NAD-ME (malic desidrogenase dependent of nicotinamide adenine dinucleotide), enzyme located in the mitochondria and PCK (phosphoenol pyruvate carboxykynase), enzyme located in the cytoplasm (OSMOND, 1974).

Again, details of the foliar anatomy of grasses are related to the subtype of C4 (Figures 1-3). In general, differences among the subtypes of C4 are related to the vascular sheath of the mesophyll and the presence or absence of mestome (parenchymatic sheath) in the terminal nerves (table 1) (OSMOND, 1974; PRENDEGARST; HATTERSLEY, 1987). However, as expected, these typical structures do not fit for all C4 grasses: at least 14 distinct combinations of anatomical features and biochemical patterns have been described in different species (MUHAIDAT; SAGE; DENGLER, 2007). Eudicotyledons were found to be either NADP-ME or NAD-ME, but there are no obvious anatomical differences between them, just some ultrastructural features that eventually point out the subtype of C4 pathway (BRUHL; PERRY, 1995; MUHAIDAT; SAGE; DENGLER, 2007). Also, sedges are generally NADP-ME and present an uneven vascular sheath and a mestome that is located between the Kranz sheath and the mesophyll (TAKEDA et al. 1985; BRUHL; STONE; HATTERSLEY, 1987; UENO; KOYAMA, 1987; MARTINS; MACHADO; ALVES, 2007, 2008).

**Table 1 - Main anatomical features of the C4 subtypes in grasses**

	Vascular sheath	Mestome (parenchymatic sheath)
NADP-ME	uneven	absent
NAD-ME	even	present
PCK	uneven	present

### Leaf anatomy of CAM plants

The CAM metabolism is defined as one presenting the nocturnal fixation of carbon by PEPcase, which is stored in organic acids in the vacuoles of the cells of the mesophyll during the night. During the day, the acids are decarboxylated and the carbon is incorporated into carbohydrates via the C3 cycle. The weak CAM plants present differences, between dawn and dusk, in the titrable acidity in the order of 10 to 50  $\mu\text{Eq.g}^{-1}$  of foliar fresh mass, while the strong CAM plants, of more than 100  $\mu\text{Eq}$  of titrable acidity per gram of foliar fresh mass (GUARALNICK; JACKSON, 2001).

Worldwide, CAM plants are related to arid environments. There are two great groups of CAM plants: one of succulent plants of arid regions and epiphytes from humid (sub)tropical regions (EHLERINGER; MONSON, 1993), but there are some water plants that also carry out the CAM cycle (KEELEY, 1998).

Some species are able to carry out both CAM and C3 metabolisms, in such a way that there is a great variability of behaviours of CAM (KLUGE; TING, 1978; FRANCO et al. 1994; NIEVOLA et al., 2005):

- a) the typical CAM plants: only assimilate carbon during the night period
- b) plants that assimilate atmospheric carbon during both day and night
- c) the idle CAM plants: do not assimilate atmospheric carbon, just using the CAM metabolism to recycle the internal carbon (generally, cacti during extremely dry periods)
- d) plants that only start nocturnal carbon assimilation when exposed to water stress
- e) plants whose young leaves are C3, the CAM cycle being expressed only in the mature leaves.

Regarding the leaf anatomical features of the CAM plants, there is not a specific pattern of organization of the mesophyll, so the leaves tend to follow the anatomical pattern of the families to which the plants belong. In common, the CAM leaves must present vacuoles large enough to store the organic acids produced during night-time without injuring the enzymes of the cytoplasm (KLUGE; TING, 1978; GUARALNICK et al. 2002). Therefore, the CAM leaves must present succulence, a morpho-anatomical attribute for leaves containing high reservoirs of water. Again, the structure precedes the function: all CAM or intermediate C3-CAM plants present some degree of succulence, but most species of succulent leaves are C3 (KLUGE; TING, 1978).

Evidently, all leaves store some amount of water, and the question is to estimate an index that could indicate a higher degree of succulence, under which the CAM metabolism would not be possible. The most appropriate index has been the ratio, for each unit of leaf area, of the water amount (in grams) and the content of chlorophyll (in milligrams). Values above 1,0 indicate a succulent leaf and, thus, able to perform the CAM metabolism (KLUGE; TING, 1978; GUARALNICK et al. 2001; NIEVOLA, 2005). However, such an index needs to be better validated, mostly in the case of weak CAM plants.

## The leaf scleromorphism

Leaf anatomy may also reflect photosynthetic adaptations to unfavourable environments (PAVIANI, 1984): in tropical ecosystems submitted to high solar irradiances and some degree of water deficit (savannahs, deserts, rocky mountains, dunes, sandbanks, etc.) are commonly found species with foliar scleromorphism (table 2). Notwithstanding, the soils of such areas are commonly acid, poor in nutrients and with a high content of aluminum and other heavy metals (ARENS, 1958; PAULA, 1978; DEMMIG-ADAMS; ADAMS, 1992).

**Table 2 - Leaf scleromorphic characteristics**

Thickness of the leaf	more than 100 $\mu\text{m}$
Epidermis	hairy
Cuticles	thick
Epidermal cell walls	silica incrustated
Stomata	high density, immersed in crypts

In spite of the thick cuticles and thicker wall of the epidermal cells, such leaves do not necessarily present a low cuticular transpiration: there are some species whose cuticular transpiration may represent up to 30% of the total transpiration, while other species present a low cuticular transpiration that is less than 2% of the total transpiration (FERRI, 1944; RAWITSCHER, 1948; ARENS, 1958). In the same way, the stomata do not necessarily carry out an efficient transpiration control: there are species with scleromorphic leaves that present a very slow stomata closure even after being detached from the plant, while there are plants with higromorphic leaves able to present a fast stomata closure after detachment (FERRI, 1944).

The best explanation for the adaptive advantages of scleromorphism is the high degree of light reflectance, and the soil conditions appear as a confounding variable. Since such leaves reflect a greater amount of the excessive solar light of such environments, the scleromorphic leaves would attenuate the excessive incident light over the photosystem, conferring protection against photodamage (DEMMIG-ADAMS; ADAMS, 1992; JORDAN; DILLON; WESTON, 2005). Studies in meteorological towers have measured, in the whole vegetation, the ratio of the incident solar light and the carbon assimilation rate: both the Cerrado and the Mediterranean vegetation, that have a great prevalence of species with scleromorphic leaves, show a high reflectance of the solar light: 70 fotons are required for the assimilation of one carbon dioxide molecule, while humid tropical forests require only 20 fotons (MIRANDA, 1997).

Anyway, in some of these environments, plants with foliar scleromorphism (MORRETES, 1967, 1969) exist alongside plants with leaves typical of humid environments (PALHARES, 2003), indicating that many types of functional adaptations are able to overcome the environmental adversities.

## Amphystomy and photosynthetic responses

Another feature actually present and not fully understood is the amphystomy, which only occurs in leaves thicker than 100  $\mu\text{m}$  (PARKHUST, 1978). Species with amphystomatous leaves are more common in environments submitted to high solar irradiances. With regard to the availability of water, amphystomy is observed in mesic, xeric and humid environments, but presents a higher prevalence in mesic environments, suggesting an advantageous adaptation (PARKHUST, 1978).

For species from the same genus, for a given transpiration rate, the carbon assimilation rate would be higher in amphystomatous leaves, which means amphystomy would be related to a higher water use efficiency. In humid environments, the hipostomatous plants would be in their optimum of water use efficiency and the amphystomy would thus not be of any great advantage. In the same way, in dry environments, all plants must save water so amphystomy would not be so advantageous. But in the mesic environments, amphystomy would provide a more competitive water use efficiency, which could explain the greater prevalence of amphystomy in such environments (PARKHURST, 1978; KEBEDE et al., 1994).

Another explanation for the amphystomy would be the optical behaviour of the leaf: each one of the epidermal cells presents a slight convexity, making the leaf epidermis to be an astigmatic lens. Also, the cell walls of the mesophyll canalize the light through total reflection in such a way, and especially when only illuminated by diffuse light, that there is a light gradient in the mesophyll layers inside the leaf, which varies according to the angle of light incidence. The amphystomy would thus be a way to provide atmospheric carbon dioxide via stomatal conductance to the mesophyll layers that present the greatest photon flux density, considering the variation of the solar angle between morning and afternoon which would explain the greater prevalence of amphystomatous species in environments of high lighting (TERASHIMA; HIKOSAKA, 1995; PALHARES, 2009).

Also, amphystomy is a plastic phenomenon: shaded leaves of amphystomatous species may present a thin hypostomatous leaf blade (MOTT; MICHAELSON, 1991). The relationship between amphystomy and the reflects on equations for estimating stomatal conductance has been a recent matter of study. Stomatal conductance is not the same in abaxial and adaxial surfaces and the angle of solar incidence may stimulate either one or the other surface in maize (ANDA; LOKE, 2002)

### III. General conclusions

The C4 plants were in general more studied regarding the relationship on anatomical features related to the photosynthetic profiles than the CAM plants. While the first authors (LAETSCH, 1974) reported the classic paradigm of Kranz anatomy with C4 cycle, indeed the rising knowledge on these groups has disclosed a variety of degrees of anatomical organisation and of photosynthetic profiles, which reflects the small and continuous modifications of the species throughout their stories. However, the other peculiar anatomical structures, such as the scleromorphism and amphystomy, rest to be deeper studied for a general theory about them.

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