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A Comparative Study of the Leaf Anatomy of the Grasses *Andropogon ischaemum* and *Chrysopogon gryllus*

By

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With 14 Figures (5 Plates)

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Summary

The leaf anatomy of the grasses *Andropogon ischaemum* and *Chrysopogon gryllus* was studied at the level of light and electron microscopy. These species are dominating the foot-hill grassland of Northern Greece. The volume of the intercellular airspace system of their leaves was estimated as well.

The observations show that both plants have a xeromorphic appearance and belong to the C_4 photosynthetic species, because they bear all the characteristics of the Kranz syndrome. The leaves of *A. ischaemum* have a water storing parenchyma at the top side of the midrip which is absent in *C. gryllus*. The bundle sheath cell chloroplasts of *A. ischaemum* bear a great quantity of starch and entirely lack grana, while the corresponding chloroplasts of *C. gryllus* bear rudimentary grana, but their starch content is far smaller. The cells of the assimilative mesophyll are arranged around the vascular bundles. This arrangement in *A. ischaemum* is more regular, the cells are elongated and with relatively small intercellular spaces; on the contrary, in *C. gryllus*, the intersections of these cells are almost circular, resulting in wider intercellular spaces. The chloroplasts of the mesophyll cells in *A. ischaemum* have peripheral reticulum and better developed grana than in *C. gryllus*. All these differences indicate that *A. ischaemum* is better adapted to withstand adverse environmental conditions than *C. gryllus*.

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Zusammenfassung

Die Blattanatomie der Gräser *Andropogon ischaemum* und *Chrysopogon gryllus* wurde licht- und elektronenmikroskopisch untersucht. Diese Gräser sind im Grasland der Vorgebirge Nordgriechenlands vorherrschend. Ferner wurde das Interzellularvolumen der Blätter bestimmt. Die Beobachtungen haben ergeben, daß beide Pflanzen von xeromorphem Bau sind und zu den C_4-Pflanzen zu rechnen sind, da sie alle Charakteristika des Kranz-Typus zeigen. Die Blätter von *A. ischaemum* besitzen ein wasserspeicherndes Parenchym über der Mittelrippe, welches bei *C. gryllus* fehlt. Die granalosen Chloroplasten der Bündelscheiden von *A. ischaemum* führen reichlich Stärke, während die entsprechenden Chloroplasten von *C. gryllus* rudimentäre Grana und viel weniger Stärke enthalten. Die Zellen des assimilierenden Mesophylls sind um die Gefäßbündel angeordnet, bei *A. ischaemum* regelmäßiger, mit länglichen Zellen und relativ wenig Interzellularen, bei *C. gryllus* hingegen sind diese Zellen von eher kreisförmigem Querschnitt, die Interzellularräume sind dadurch weiter. Die Mesophyll-Chloroplasten von *A. ischaemum* besitzen ein peripheres Reticulum, die Grana sind besser ausgebildet als in *C. gryllus*. Die Unterschiede deuten darauf hin, daß *A. ischaemum* ungünstigen Umweltbedingungen besser angepaßt ist als *C. gryllus*.

(übers. vom Editor).

Introduction

The photosynthetic system in plants follow two schemes fundamentally. The one of them is known as C_3 photosynthesis and the plants in which it takes place are called C_3 plants (Calvin & Bassham 1962); the other scheme is known as C_4 photosynthesis and the plants in which it takes place are called as C_4 plants (Kortschak, Hartt & Burr 1965, Hatch & Slack 1966). C_4 plants are characterized by the presence of a parenchymatous bundle sheath around the vascular bundles, which was termed as "Kranz" by Moser 1934 and all C_4 plants are known as Kranz plants. C_3 plants, which lack this characteristic sheath, are known as non-Kranz plants. In addition to this, C_4 plants display other physiological, anatomical and cytological features of the leaves as well, all of which constitute the Kranz syndrome (Downton & Tregunna 1968, Tregunna *et al.* 1970, Frederick & Newcomb 1971, Johnson & Brown 1973). Among the Gramineae about half of them are C_3 (non-Kranz) and the other half are C_4 plants (Kranz) (Smith & Brown 1973).

Andropogon ischaemum L. and *Chrysopogon gryllus* (L.) Trin are two economically important grasses because they dominate the grasslands of the Central and Northern Greece. They are drought resistant, less demanding in soil fertility and highly competitive. They grow during the summer period when rainfall is limited. Moreover, they are highly productive although

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their nutritive value for the grazing animals is fair (HITCHOK 1950, LIACOS & BISWELL 1977).

The ecology of these two species, especially in comparison to each other, has not been studied yet under the Greek conditions to the best of our knowledge. However, it appears that *A. ischaemum* is more widespread and better adapted to the relatively dry summer conditions of Northern Greece than *C. gryllus*.

The purpose of this study was to compare the anatomy of leaves of these two grasses at the level of light and electron microscopy and relate their differences to their potential to withstand unfavorable environmental conditions.

Materials and Methods

The plants of *A. ischaemum* and *C. gryllus*, used in this study, were taken from populations of both species established at the University of Thessaloniki Forage Plants Garden. These populations represented collections of accessions from all over the Northern Greece.

For preparation of the tissues for both light and electron microscopy whole plants were carried in the laboratory in the month of April, when the species were at their early growth stage. The last expanded leaves were cut and immersed at once in KARNOVSKY's 9% glutaraldehyde-paraformaldehyde fixative (KARNOVSKY 1965) in a 0.05 M sodium cacodylate buffer, pH 7.1, for 3 hours at room temperature. The material was cut in small pieces while immersed in the fixative. After several washes in buffer, the material was post-fixed in buffered 2% osmium tetroxide for 2 hours, also at room temperature, dehydrated in a graded acetone series and propylene oxide, and embedded in SPURR's low viscosity epoxy resin (SPURR 1969). Thin sections were cut on a REICHERT OmU_2 ultramicrotome, stained with uranyl acetate and lead citrate (REYNOLDS 1963), and then viewed and photographed with a JEM 100-B (JEOL) electron microscope. Semithin sections of plastic embedded tissue were used for light microscopy, after staining with 1% toluidine blue 0 in 1% borax solution, or without any staining.

For measuring the volume of intercellular airspace systems of leaves a method of water infiltration was used, similar to that described by BYOTT 1976.

Results

Intercellular airspace volume

The volume of the intercellular airspaces of fresh leaves in *A. ischaemum* was estimated to be 0.12 ml/gr of leaf, while in *C. gryllus* 0.30 ml/gr of leaf.

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Light microscopy

In a transverse section of a leaf the two plants present many anatomical similarities, but certain differences exist as well (Figs. 1, 2 [3])).

Among the epidermal cells in both species, especially on the adaxial epidermis (AdE), there are certain cells which are much bigger in volume than the rest, with thin walls. These cells have very large vacuoles and are known as bulliform cells (Figs. 1a, b: BC) (Fahn 1974). An observation of unstained sections in crossed Nicols (Figs. 1b, 2b) shows that the bulliform cells are not lignified. Stomata (St) are found especially on the abaxial epidermis (AbE), while on the adaxial one very few are observed (Figs. 1, 2).

Most of the mesophyll is occupied by the vascular tissue and the accompaning elements. The vascular bundles are surrounded by large, sphaerical or oval cells, connected with each other in such a way that they form a sheath, the bundle sheath (BS), known as Kranz. Their cell walls are very thick and lignified (Figs. 1a, 2a). The well developed chloroplasts of the Kranz cells are distinct, with many large starch grains in *A. ischaemum* (starch sheath), but not in *C. gryllus*. In both plants the Kranz cells are surrounded by unlignified mesophyll cells (Figs. 1a, 2a: MC), with many chloroplasts generally lacking starch. Even though their arrangement around the bundle sheath is radiated in both plants, in *A. ischaemum* it is more regular, and the cells are more elongated (Fig. 1a: MC); this looks like a transitory condition towards or from the palisade parenchyma of the typical leaves of dicots. On the contrary, in *C. gryllus*, a greater disorder is observed (Fig. 2a: MC), with many circular transections of these cells, and therefore larger intercellular spaces; this reminds more of the spongy parenchyma of the leaves of dicots.

Towards the upper side of the midrip in *A. ischaemum* many large, cylindrical or polygonal parenchymatic cells are developed, without or with very small intercellular spaces, with relatively thin and to a certain degree lignified walls (Figs. 1a, b: WP). Some of these cells are found in direct contact with xylem — they are separated from the vessel elements only with the bundle sheath cells (Fig. 1a) — and their sum composes a strand that runs along the leaf, parallel to the vascular tissue and the sclerenchymatous strand (SS). These cells resemble the bulliform epidermal cells. In *C. gryllus*, on the contrary, in the corresponding position of the leaf, these cells do not exist (Fig. 2a).

The adaxial epidermal cells of the central area of the leaf in *C. gryllus* are of the bulliform type (Figs. 2a, b: BC). Below them there is a layer of smaller, fine-walled, colourless, unlignified cells, which are found in the rest of the leaf plate as well. Just below the two central bulliform cells in the middle of the leaf, a lignified cell is observed (Figs. 2a, 2b).

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[3]) A list of the abbreviations used in the figures see p. 35).

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Electron microscopy

The cells of the bundle sheath (BSC) (starch sheath) are closely connected to each other and form an entirely closed ring around the vascular tissue (Kranz sheath). They have uniformly thickened walls, in which the lamellate structure is clearly distinguishable (Figs. 3, 5). This appearance is observed in both plants, even though the walls in *C. gryllus* are somewhat thinner. Inside this wall in both plants an electron opaque layer is observed, which surrounds completely the cell in the external side and extends itself almost to the whole of the anticlinal walls (Figs. 3, 4, 5, 9: SL). In the anticlinal walls the two layers from the two adjacent cells, proceed alongside, without, however, uniting themselves with each other, while they disappear inwardly (Figs. 3, 4, 5, 13). This layer is absent entirely from the internal walls. In a greater magnification it presents a characteristic structure, two electron-dense lines bounding a region of lower electron density (Figs. 4, 9, arrows). O'Brien & Carr 1970 observed this layer in the walls of some other monocots and called it a "suberized lamella", since they proved that it is composed of suberin.

The bundle sheath cells communicate with their neighbouring cells, as well as between them, by means of numerous plasmodesmata, gathered together at certain places forming pit fields. At these positions, the cell walls remain far more unthickened (Figs. 3, 4, 6, 7, 13, 14: PF). The pit fields are especially developed and are found at a significantly greater number on the external walls, neighbouring to the mesophyll parenchyma cells. The frequency of their appearance on the anticlinal walls is small and even smaller on the internal wall, neighbouring to the vascular parenchyma cells. Communication through plasmodesmata between the bundle sheath cells, on one hand, and the vessel or sieve elements, on the other, was not observed, even though both cells are very often found in contact. The structure of the suberized lamella (SL) within the pit fields of the external walls is different from the one that has been discribed up to now, as it is composed from many thin lamellae, which seem to constrict the plasmodesmata forming a distinct waist (Fig. 6, arrows). The pit fields on the anticlinal (Fig. 4) and internal walls (Figs. 13, 14) are simpler, because the suberized lamella either does not extend itself at all towards them (it is entirely absent from the internal walls) or presents a very simple structure. The pit fields of the mesophyll cells have a much simpler structure (Fig. 10: PF), while the pit fields of the large cells over the midrip in *A. ischaemum* show a somewhat more complicated structure (Fig. 7).

In the bundle sheath cells the chloroplasts constitute the most evident organelle and they frequently occupy the greatest part of the cell lumen (Fig. 3). In *A. ischaemum* the bundle sheath chloroplasts bear a high number of starch grains of various sizes (Figs. 3, 4: S). On the contrary, in *C. gryllus* starch grains are almost absent (Figs. 5, 9). In *A. ischaemum*

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these chloroplasts bear a great number of membranes that run alongside, without, however, gathering together at certain positions to form grana (Fig. 8). In *C. gryllus*, however, an attentive observation shows that in the bundle sheath chloroplasts there are few rudimentary grana (Fig. 9: G), constisting of 2—5 lamellae and thylakoids. In *A. ischaemum* these chloroplasts have a denser stroma and more lamellae than in *C. gryllus* (compare Figs. 8, 9).

The chloroplasts of the mesophyll cells bear grana in both plants (Figs. 10, 11, 12). In *A. ischaemum* the grana are more clear and better developed (Fig. 12), while in *C. gryllus* they are less distinguishable from the rest membranic system of the organelle (Fig. 11). In many mesophyll chloroplasts there is no starch at all, especially in *C. gryllus*. In *A. ischaemum* very few starch grains are sometimes observed (Figs. 10, 12: S). These differences in the structure of the chloroplasts in the same leaf constitute a structural dimorphism.

The mesophyll cell chloroplasts in *A. ischaemum* bear a moderately developed membrane system of anastomosing tubules in the peripheral stroma, which has been termed peripheral reticulum (PR) (Laetsch 1968). The PR was observed in all chloroplasts with grana in *A. ischaemum* (Figs. 10, 12). In *C. gryllus*, its appearance is limited; it is observed, however, in all chloroplasts in the form of a few isolated vesicles. It is harder to distinguish in the agranal chloroplasts of the bundle sheath in *A. ischaemum* (Figs. 4, 8).

Mitochondria are small, with shape ranging from sphaerical to oval, with regular development of internal membranes. Their appearance is the same in the mesophyll and bundle sheath cells, while in number there are somewhat more in the last cells. A greater number of mitochondria is observed in the cytoplasm within the pits (Figs. 4, 14: M). No mitrochondrial dimorphism, as in chloroplasts, was observed.

Microbodies are small, usually spherical, without internal structures, surrounded by a single membrane. More microbodies were observed in the bundle sheath cells than in mesophyll cells, however, without this difference being great. The microbodies are frequently closely connected with chloroplasts, mitochondria and membranes of endoplasmic reticulum (ER) (Fig. 13: Mb). This connection is especially obvious in the bundle sheath cells than in the mesophyll cells, where the microbodies seem to be more independent (Fig. 10: Mb). It is possible, however, that the points of contact may be found at a different level from that under observation, as this appears in the study of serial sections (Fig. 10). In the cases where there is actually no contact, it is possible that ER undertakes a connecting role.

The appearance of endoplasmic reticulum is generally limited; it is often found on both sides of the pit fields (Figs. 6, 14: ER). In certain cases,

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vesicles of ER are observed within the plasmodesmata, which indicates that it is continuous in two adjacent cells.

Discussion

The results show that both grasses *A. ischaemum* and *C. gryllus* have the Kranz anatomical characteristics and therefore belong to the C_4 plants. For *C. gryllus* especially, the same result is reported by Brown & Gracen 1972 and Smith & Brown 1973.

The study of the leaf anatomy, especially in the light microscope, shows that both plants have a clearly xeromorphic structure (Figs. 1, 2), which, in combination with the physiological functions, may render them capable to grow in dry and arid areas.

The presence of the suberized lamella in the external and anticlinal walls of bundle sheath cells (Fig. 3) may have a physiological significance for the movement of water and solutes, because suberin is considered generally to be impermeable to them (O'Brien & Carr 1970). If this is the case, the water supply of all tissues outside the bundle sheath must take place necessarily through the plasmodesmata and consequently the water movement may be regulated by the vital activity of the plasma. This control might be essential if an adequate supply of water is to be maintained to the leaf tip, especially in the dry areas where these plants grow. The water offered to these long leaves could be easily transpired by the lower half of the leaf, without ever reaching the tip.

Since suberized lamella is impermeable to water and solutes, the only one pathway through the external walls must be the symplastic one. On the contrary, in the internal walls both symplastic and apoplastic transfer must occur. The apoplastic pathway must be followed for the movement of substances between the bundle sheath cells and the vessel or sieve elements, in whose common walls were not observed any plasmodesmata, even though an indirect symplastic movement is also possible through the vascular parenchyma cells. This absence of plasmodesmata, as well as the absence of the suberized lamella from the internal walls, is contrary to the observations in the cell walls of mestome sheath of C_3 plants, where exists the suberized lamella (O'Brien & Carr 1970), as well as the plasmodesmata (Kuo, O'Brien & Canny 1974) and the only possible movement must be the symplastic one. For this reason the functional significance of the bundle sheath in C_4 plants must not be exactly the same as that of the mestome sheath of C_3 plants, from certain aspects at least. This lamella, at positions where it exists, must be a barrier against the free apoplastic movement of the water and assimilates and permits the cell to have an active regulation of the transfer of substances. The frequent presence of mitochondria in the cytoplasm within the pits (Figs. 4, 7, 14: M) suggests that these organelles supply energy for an active transfer.

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The chloroplasts of the leaves of *A. ischaemum* and *C. gryllus* present a dimorphism (compare Figs. 4, 12 and 5, 11). The structural dimorphism is very pronounced, while the size dimorphism is harder to distinguish. The most obvious hypothesis, concerning the structural dimorphism, is that the increased amount of stroma in chloroplasts of the bundle sheath, with the simultaneous decrease of lamellae in comparison to the mesophyll chloroplasts, is related to starch synthesis. For this reason, many researchers consider them as structural and/or functional amyloplasts (Laetsch 1974) and the bundle sheath as "starch sheath", even though there exist opposite oppinions on this (Black 1973). The detection of many and large starch grains in *A. ischaemum* (Figs. 3, 4: S) and their almost complete absence from *C. gryllus* (Figs. 5, 9), although both plants were developed and treated under precisely the same conditions, gives rise to the hypothesis that the difference may be related to the absence or presence of grana, correspondingly. If this is true, then the view expressed by Johnson & Brown 1973, that these positions are "functionally trivial" should be reconsidered. If these rudimentary grana may play such an important role, this structural dimorphism of chloroplasts might be responsible for their different action.

The function of bulliform cells is related to the unfolding of the young leaves, or to the rolling or unrolling of mature leaves as a result of loss or uptake of water (Fahn 1974). In *A. ischaemum* the cells that are found at the centre of the leaf exactly above the midrip (Fig. 1a: WP), are considered to serve as storage of water, because they have all the features of a water storing tissue. The slight lignification of their walls and their place inside the leaf show that they may not be related or that they are slightly related to the rolling of leaves, but that they may constitute almost exclusively a water storing tissue. This water is used in cases of water stress. As they are bordering with the vessel elements, the quick acquisition of water is easy during the rain falls. The absence of this tissue from the leaves of *C. gryllus* (Fig. 2a) suggests that this plant is less drought resistant than *A. ischaemum*. Possibly, in *C. gryllus* a role of water storage might be undertaken by the adaxial epidermal cells of the central area of the leaf (Fig. 2a), whose features are similar to that of bulliform cells. Furthermore, as the intercellular space system in *A. ischaemum* is smaller than in *C. gryllus*, this may be an indication that the photosynthetic activity of the former is more intense, while the water loss may be more restricted (Byott 1976), than that in the latter.

It is known, that the peripheral reticulum (PR) increases the surface of the inner membrane of the chloroplast envelope and it has been suggested that it is involved in rapid transport of photosynthetic precursors or end products between cytoplasm and chloroplasts (Laetsch 1971, 1974). Since the mesophyll chloroplasts of *A. ischaemum* have this reticulum more deve-

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loped, this suggests an increase in the shuttling of products between chloroplasts and cytoplasm.

It can be concluded that the better structure of leaves of *A. ischaemum*, in terms of water storing parenchyma, intercellular airspaces, starch grains, grana and peripheral reticulum as compared to *C. gryllus*, indicates that the former species has a greater potential for growing in unfavorable environmental conditions, than the latter.

Abbreviations used in figures: AbE = abaxial epidermis; AdE = adaxial epidermis; BC = bulliform cell; BS = bundle sheath; BSC = bundle sheath cell; Cl = chloroplast; ER = endoplasmic reticulum; G = grana; LB = lipid body; M = mitochindrion; Mb = microbody; MC = mesophyll cell; N = nucleus; P = plasmalemma; PF = pit field; PP = phloem parenchyma cell; PR = peripheral reticulum, S = starch grain; SL = suberized lamella; SS = sclerenchymatous strand; St = stoma; T = tonoplast; V = vacuole; VE = vessel element; W = wall; EW = external walls of bundle sheath cells; AW = anticlinal walls of bundle sheath cells; IW = internal walls of bundle sheath cells; WP = water storing parenchyma; XP = xylem parenchyma cell.

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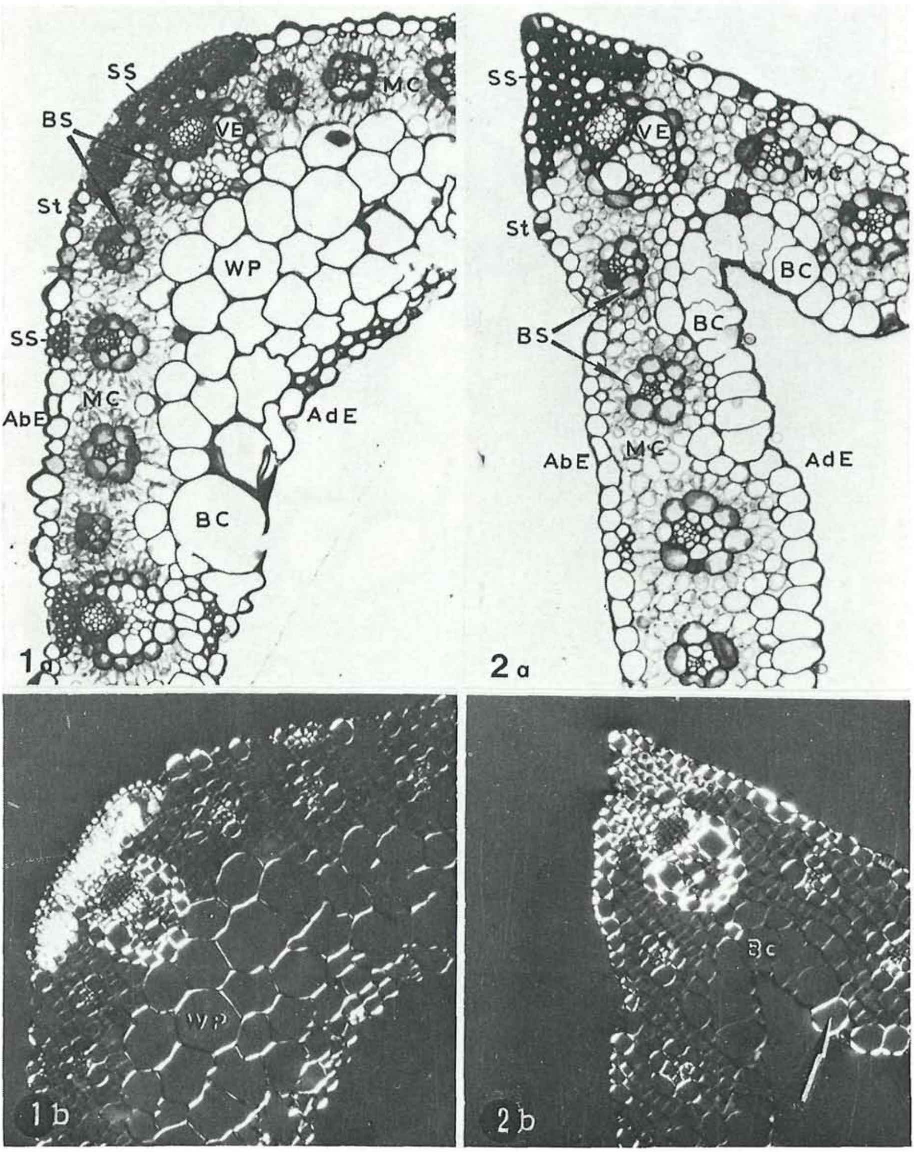

Figures

Figs. 1a, b. Transverse sections in the central region of *A. ischaemum* leaf. 1b, between crossed Nicols; the lignified areas are birefringent × 160

Figs 2a, b. Transverse sections in the central region of *C. gryllus* leaf. 2b, between crossed Nicols. The central adaxial epidermal cells exhibit the characteristics of bulliform cells (BC); their walls are not lignified, in contrast with the other epidermal cells (2b, arrow) 2a: × 205, 2b: × 160

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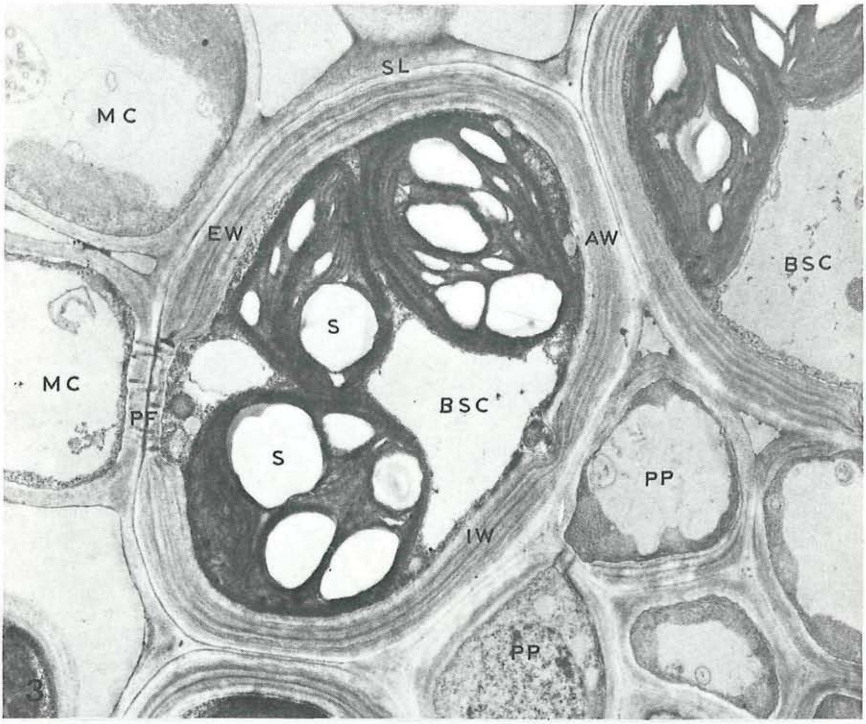

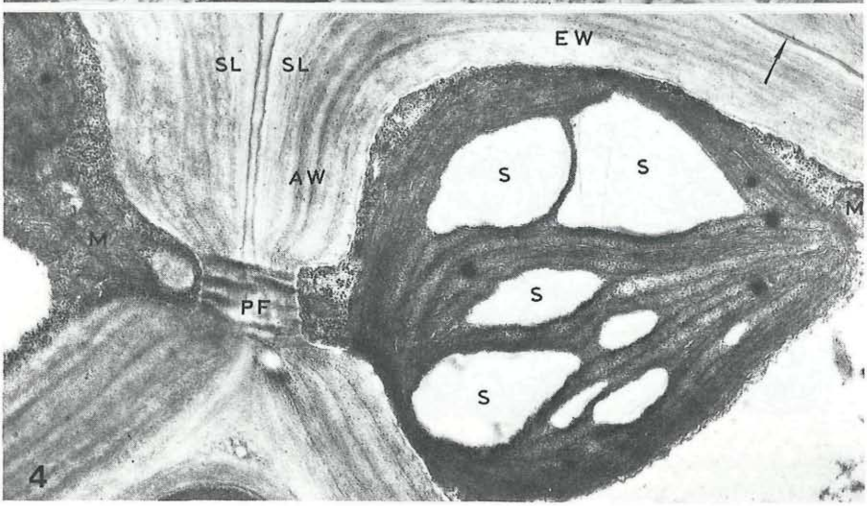

Fig. 3. A transverse section of a bundle sheath cell (Kranz cells) of *A. ischaemum*, with distinct starch grains (S) in the chloroplasts and uniformly thickened walls (EW, AW, IW). × 5.000

Fig. 4. A chloroplast of a bundle sheath cell of *A. ischaemum*. In the anticlinal walls (AW) the suberized lamellae (SL) go parallel, but without joining each other. × 13.000 (Abbrevations *see* table 1)

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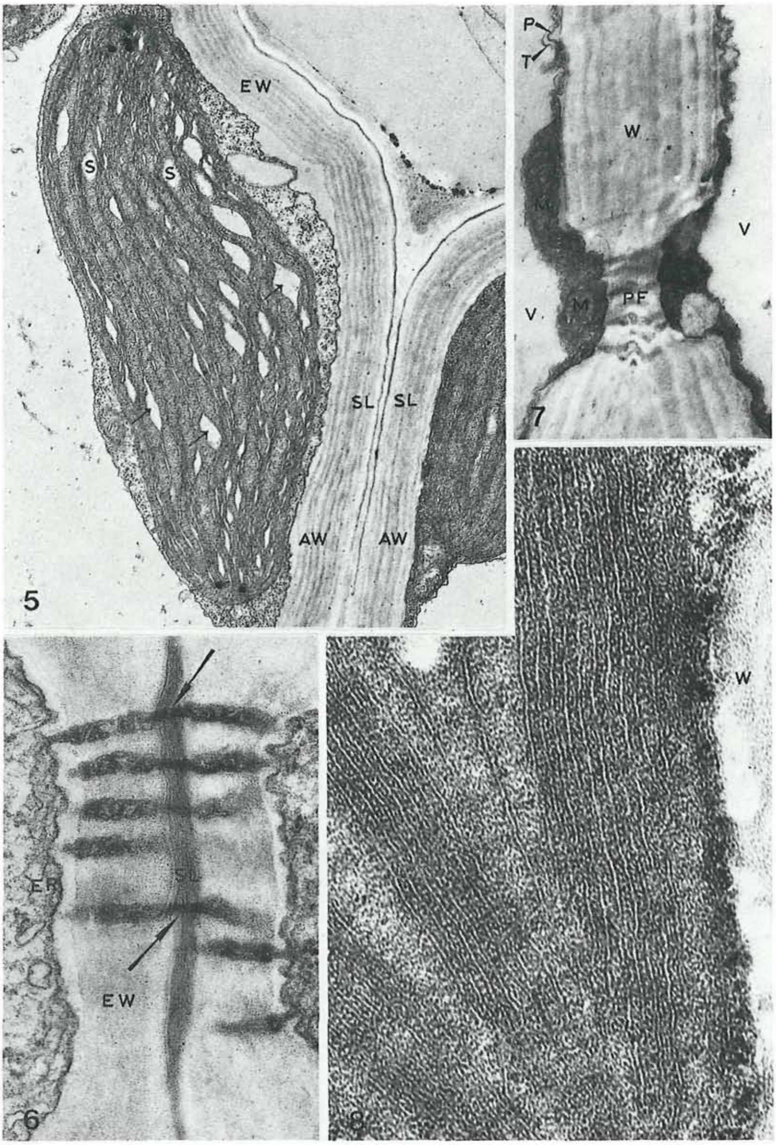

Fig. 5. A chloroplast of a bundle sheath cell of *C. gryllus*, with swollen membranes at most places (arrows). There are very few minute starch grains (S). × 12.000.

Fig. 6. A pit field in the external wall (EW) of a bundle sheath cell of *A. ischaemum*. The arrows indicate the constrictions of the plasmodesmata at the crossing regions with suberized lamella (SL). ×40.000.

Fig. 7. A part of cell wall (W) of water storing parenchyma cells with a very thin parietal cytoplasm and a few organelles. ×13.000.

Fig. 8. A part of a bundle sheath cell chloroplast of *A. ischaemum*. ×63.000

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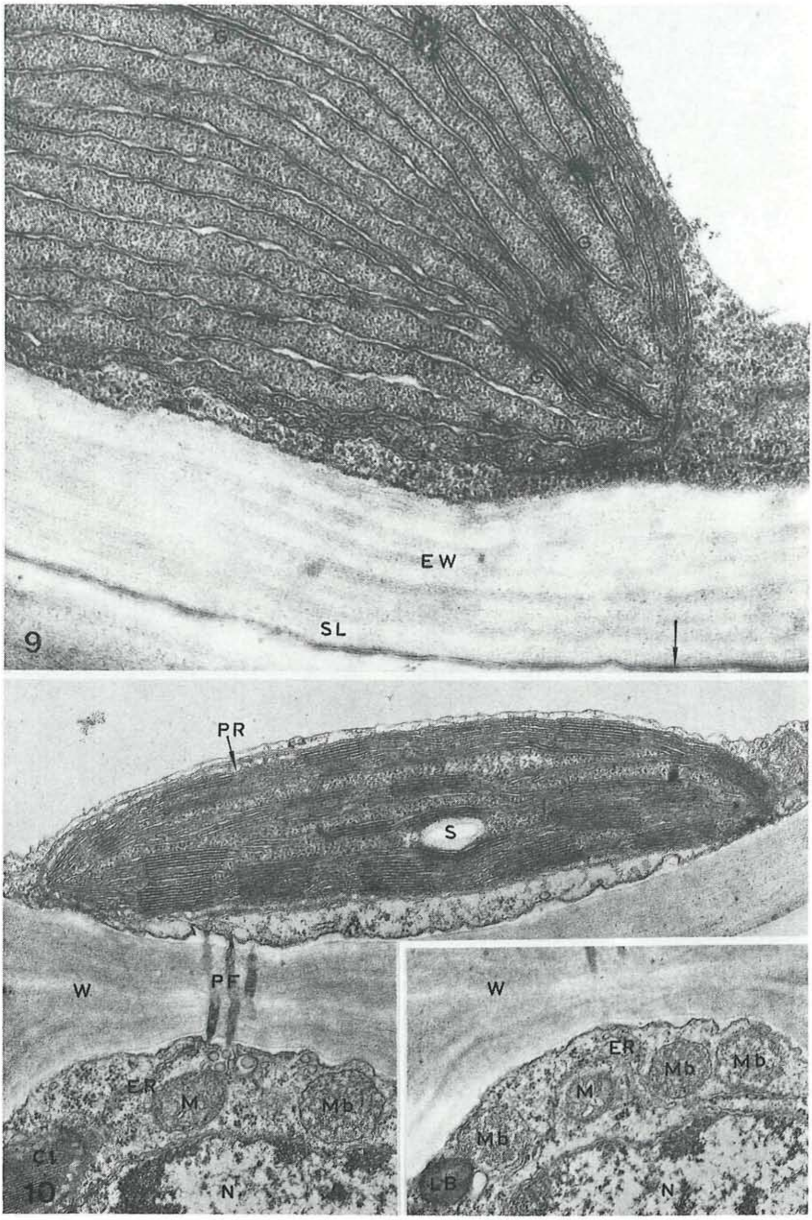

Fig. 9. A part of a bundle sheath cell chloroplast of *C. gryllus*. ×40.000.
Fig. 10. A mesophyll cell chloroplast of *A. ischaemum*. In the adjacent cell note a mitochondrion (M), a microbody (Mb), endoplasmic reticulum cisternae (ER) and part of a chloroplast (Cl) and of the nucleus (N). The inset shows part of this figure in another serial section, where there are three microbodies (Mb), but the chloroplast is absent. ×19.000. Abbreviations see italics table 1.

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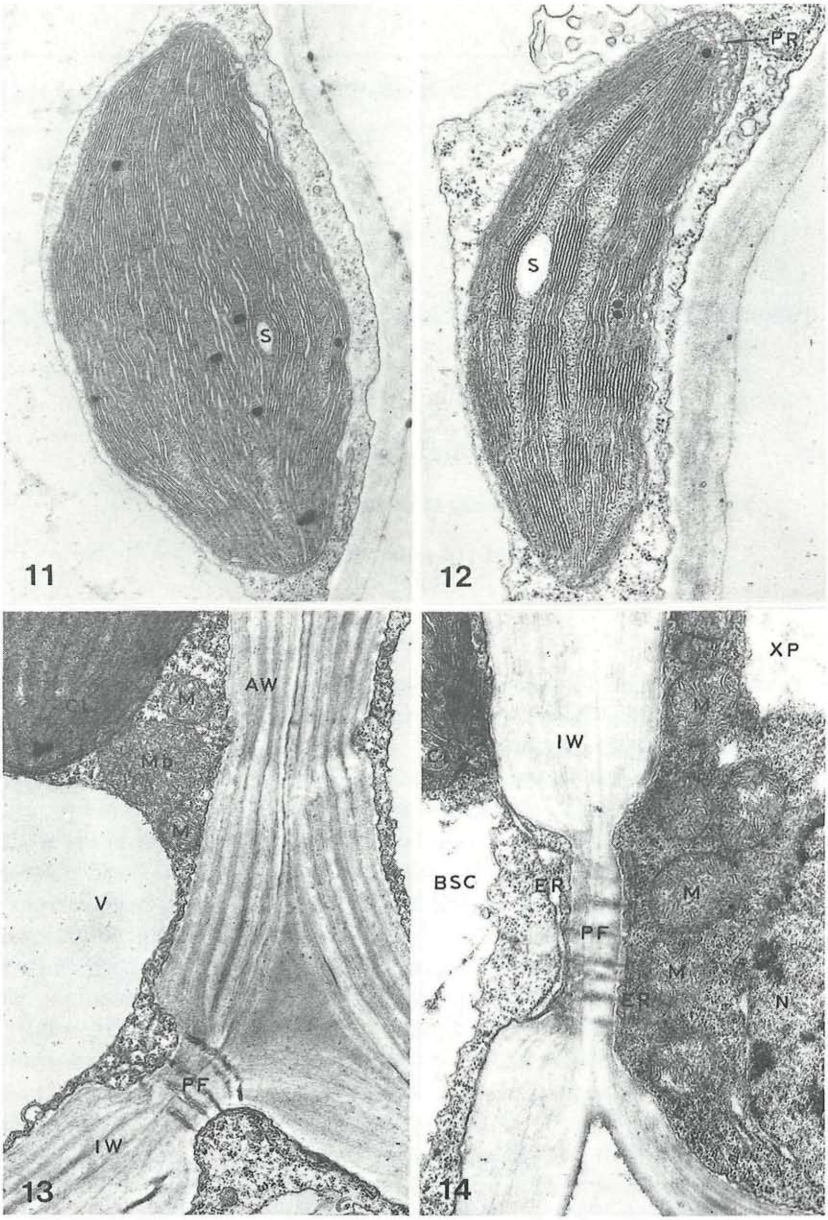

Fig. 11. A mesophyll cell chloroplast of *C. gryllus*. ×13.000.

Fig. 12. A mesophyll cell chloroplast of *A. ischaemum*, with a relatively developed peripheral reticulum (PR). ×17.000.

Fig. 13. A large microbody (Mb) in a bundle sheath cell of *A. ischaemum*, very close to a chloroplast (Cl) and two mitrochondria (M). ×10.800.

Fig. 14. A part of the wall (IW) between a bundle sheath cell (BSC) and a xylem parenchyma cell (XP), with many mitrochondria (M) in the parenchyma cell. ×20.000. Abbreviations *see* table 1.

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