

THE ANATOMY OF ANOMALOUS GRASS
HYMENACHNE AMPLEXICAULIS

JAMES L. HAYNES, Indiana University

In the grasses two general types of arrangement of vascular tissue are found. The most familiar system of arrangement is that found in corn in which the bundles are scattered throughout the transverse section of the stem. In the other arrangement the bundles are confined to a zone surrounding the hollow center of the culm as exemplified in wheat. Those grasses having the vascular tissue confined to a peripheral zone generally have a hollow center except in the portion of the axis bearing the inflorescence.

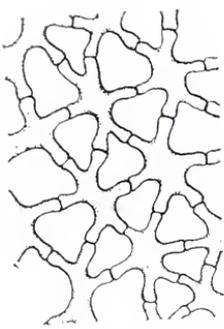
In examining herbarium specimens it has been noticed that the culm of *Hymenachne amplexicaulis* deviates from the usual systems of bundle arrangement in having the bundles confined to a peripheral zone while the center is apparently solid.

Hymenachne amplexicaulis Nees¹ is a tropical grass reported for Central America, the West Indies, and the floating islands of the Amazon, growing typically in habitats frequently inundated with water. An abundance of living material grown from seeds, collected by Dr. Paul Weatherwax in the lowlands of eastern Guatemala, has been available for an anatomical study.

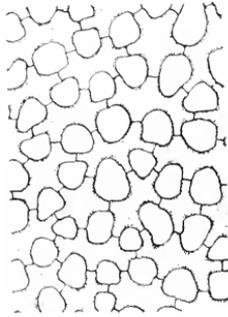
The external morphology is that of a typical grass. The internal anatomy of the aerial parts presents a system of parenchyma extending throughout the stem and leaf. In transverse section the stem shows a ring made up of sclerenchyma and vascular tissue which surrounds an aerenchymatous pith and is separated from the epidermis by aerenchymatous chlorenchyma (Fig. 1). The endostelar aerenchyma is made up of stellate cells without chloroplasts. These stellate cells adhere laterally at points of contact of the radial arms in such a manner as to form horizontal plates or diaphragms. At maturity these transverse diaphragms appear to the unaided eye as an extremely delicate lace (Fig. 8). The exostelar aerenchyma is made up of non-stellate cells containing chloroplasts and surrounding longitudinal air chambers (Fig. 2). In the leaf parallel vertical partitions of water-storage parenchyma extend the entire length of the lamina and sheath. The spaces between these walls are devoted to air chambers containing stellate aerenchyma (Fig. 3). Rows of bulliform cells are present above the air chambers in the lamina (Fig. 4).

The endostelar aerenchyma develops from the upper portion of the nodal regions. Differentiation of the aerenchyma is evident before the appearance of the protoxylem elements at the same level. Intercellular

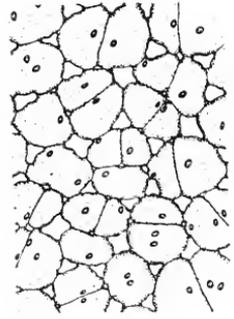
¹*Panicum amplexicaule* Rudge; *Agrostis monostachya* Poir; *Panicum hymenachne* Desv.



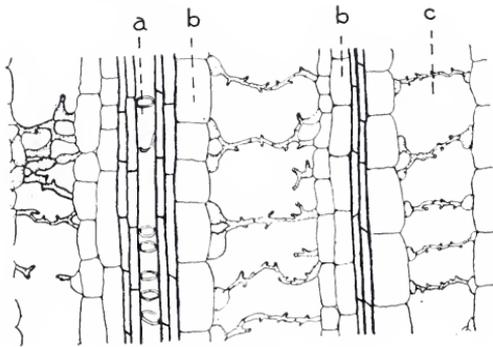
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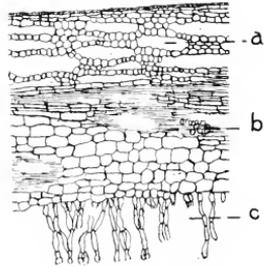
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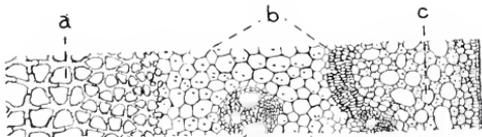
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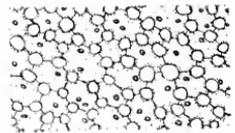
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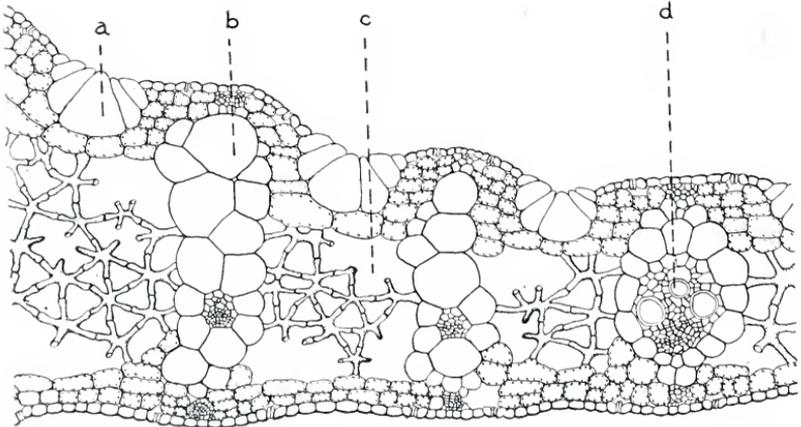
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spaces develop above the third differentiated node from the stem apex while the protoxylem appears two nodes below this point. The endostelar aerenchyma develops from "mother cells" in the nodes. At early stages of nodal development these mother cells occupy the entire internal portion of the nodal region. The first divisions of the mother cells are transverse to the stem axis. The daughter cells then undergo longitudinal division (Fig. 5). Intercellular spaces form wherever walls abut on a neighboring cell, so that finally all walls abut on intercellular spaces (Fig. 6). With enlargement of intercellular spaces to lacunae, stellate cells are formed (Fig. 7). As growth of the stem above the node exerts tension, the stellate cells pull away from their older and younger, i.e., upper and lower, neighbors in transverse diaphragms which are convex to the node from which they differentiated. Differentiation of stellate cells occurs from the center of the stem toward the periphery.

In the development of the leaf the bulliform cells and water-storage tissue are evident at an early stage and seem at no time to contain chloroplasts. In very young leaves the tissue later to become aerenchyma contains chloroplasts. Later the inner cells of this chlorenchyma enlarge and develop intercellular spaces. These spaces enlarge to form lacunae while at the same time the chloroplasts of the enlarged inner chlorenchyma cells undergo a process of disintegration. The leaf sheath is similar in general anatomy to the lamina except for the presence of bulliform cells in the latter.

It appears that physical or chemical differences in the cell walls of the older and younger generations of diaphragms may figure in the schizogenous process of diaphragm separation. Similarly, increase in the size of lacunae in the formation of stellate cells may be due in part to a change in concentration of cell sap in the maturing cells and resultant turgor differences.

Various functions have been claimed for aerenchyma. The tissue gives buoyancy to certain plants growing in water. In many plants the arrangement of diaphragms and stellate cells is such as to give maximum

Explanation of Figures

Fig. 1. Portion of transverse section of mature stem: a, endostelar aerenchyma; b, zone of vascular tissue; c, exostelar aerenchyma. X 60.

Fig. 2. Portion of longitudinal section of culm: a, exostelar aerenchyma; b, zone of vascular tissue; c, endostelar aerenchyma. X 30.

Fig. 3. Portion of longitudinal leaf section taken between the upper and lower chlorenchyma layers: a, vascular tissue; b, water-storage tissue; c, air chamber. X 125.

Fig. 4. Portion of transverse section of leaf: a, bulliform cell; b, water-storage cell; c, air chamber; d, vascular tissue. X 150.

Fig. 5. Portion of transverse section of upper nodal region. X 150.

Fig. 6. Portion of transverse section of endostelar aerenchyma taken just above Fig. 5. X 150.

Fig. 7. Transverse section of endostelar aerenchyma at stage of diaphragm separation. X 125.

Fig. 8. Portion of mature endostelar diaphragm. X 125.

support. Diaphragms are more or less water-tight and may prevent flooding of the plant in case of accidental injury.² Certain types of aerenchyma play the role of lenticels as respiratory organs while the plant is under water.³ It is generally assumed that aerenchyma serves for the storage of oxygen evolved in photosynthesis and that the aerating system is a means of transportation of this oxygen to parts of the plant body in need of it. In this plant the endostelar aerenchyma may perform the functions of flood protection and storage. The leaf aerenchyma probably contributes to mechanical support and facilitates rolling of the leaf, in conjunction with the action of the bulliform cells, when reacting to conditions of excessive transpiration.

It is interesting to note two other anomalous features of this plant, namely, that the aerenchyma cells are multinucleate and that crystalline inclusions are found in both the aerenchyma and the water-storage tissues.

Plants of this species grown from seeds in a temperate climate under mesophytic conditions have produced a fully developed aerenchyma system. This indicates that the structure is an inherited character and is not due to the immediate effect of environment. The common occurrence, however, of aerenchyma in phylogenetically widely separated hydrophytes probably has a significance that is not yet fully appreciated and which merits further study.

Acknowledgement

The writer wishes to express his appreciation to Dr. Paul Weatherwax for suggesting the problem, for furnishing the material and for his assistance in the completion of the work.

² Arber, Agnes. Water plants. pp. 183-197. Cambridge. 1920.

³ Batten, Lilly. Observations on the ecology of *Epilobium hirsutum*. Journ. Ecol. 6:161-177. 1918.