A Comparative Study of the Leaves of Lolium, Festuca, and Bromus

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A COMPARATIVE STUDY OF THE LEAVES OF LOLIUM, FESTUCA, AND BROMUS.

BY EMMA PAMMEL.

There are some striking differences in the leaves of Festuca and Lolium. One of the most essential in the species studied is the presence or absence of hairs and the involute character of the leaf of Festuca tenella.

LOLIUM PERENNÉ.

(Pl. ix, Fig. 3; Pl. xi, Fig. 8.)

*Epidermis.*—The cuticle is quite strongly developed on superior and inferior surfaces of the leaf, but more so on the inferior surface. The epidermal cells are rather large, but vary some in size; the largest occur on inferior surface of leaf and are nearly as large as the bulliform cells. The smallest epidermal cells occur chiefly at the tip of leaf. The epidermal cells above and below the stereome are smaller and are strongly thickened.

*Bulliform cells.*—The conspicuous bulliform cells number from four to five. The central are large and one or two on either side occur between each mestome bundle. The epidermal cells on the inferior surface of leaf are more uniform in size.

*Mestome bundles.*—These number eighteen, of three types. Primary bundles, those which are open on superior side of leaf, *i. e.*, where hadrome is either in direct contact with stereome or separated from it by colorless parenchyma cells, and secondary bundles or such as are closed, *i. e.*, the leptome and hadrome entirely surrounded by chlorophyll-bearing parenchyma; and third the intermediate type. The secondary mestome bundles are more numerous. The leptome and hadrome of the mestome bundle of carene are well developed. The mestome bundle of carene is of the primary type with well developed pitted vessels and spiral ducts. Two rows of thick-walled cells separate hadrome and leptome. The hadrome is separated from the
stereome by several rows of thin-walled parenchyma cells. The stereome is more strongly developed on the inferior surface of mestome bundles of carene than on superior surface of bundle. In carene the stereome is not in contact with leptome.

A thin-walled parenchyma sheath surrounds the entire bundles of secondary type. Thick-walled cells occur on the inside of this parenchyma sheath, which thus forms a sheath around the leptome and hadrome.

Two kinds of mestome bundles of secondary type occur, one in which leptome and hadrome are perfectly developed, and a second in which leptome and hadrome are not so strongly marked. Those of the second type alternate with the large bundles. These bundles are surrounded by a chlorophyll-bearing parenchyma sheath. To the inside of this sheath is a second sheath which consists of thick-walled cells (mestome sheath) surrounding the leptome and hadrome, and hence is closed. The mestome bundles of intermediate type are four in number, and do not vary from the mestome bundle of primary type except that they are closed, and there are only two pitted vessels.

Stereome.—The stereome is found on margin of leaf on superior surface of all bundles of intermediate and primary types, and on the inferior surface of some of the mestome bundles of secondary type.

Mesophyll.—This occurs between the mestome bundles, and is in contact with the epidermis on both faces. The cells are irregular, some are nearly round, others are oblong. The chlorophyll grains are large. The cells of the mesophyll on margins of leaf are somewhat smaller than in other parts.

FESTUCA.

Two species of Festuca were studied. Festuca elatior, variety pratensis, and Festuca tenella.

Beal quotes Hackel’s statement as to the different forms of Festuca: "Hackel finds the mesophyll and fibro vascular bundles quite uniform with all sorts of treatment of the plants, but the epidermis offers remarkable differences, especially that on lower surface of leaf. This difference is apparent in the thickness of the outer walls, the size of the cavities, and the existence or absence of projections on the partition walls. The dry cultivated plants had their epidermis strongly thickened toward the outside, the cavities diminished and over the partition wall
had developed cuticular projections. The moist cultivated plants produced slightly thickened epidermal cells, broad cavities, and no trace of cuticular projections. The sclerenchyma, or bast, varies much with different soils and amounts of moisture. Species of moist, shady habitats, show in their leaves a clear preponderance of the assimilating over the mechanical system."

These views coincide with the observation made in a study of the species here considered.

FESTUCA ELATIOR, VAR. PRATENSIS.

(Pl. ix, Fig. 1; Pl. xi, Fig. 9.)

Epidermis.—The epidermis is quite strongly developed in this species; the cuticle is more strongly developed on the inferior than superior surface. Small conical projections occur only on the superior surface of leaf. These are not very numerous. They are most numerous near the carene. The epidermal cells are quite uniform in shape; some variations occur, mostly on the superior surface. The cells of epidermis over the stereome on both superior and inferior surfaces are strongly thickened and are smaller than the unthickened epidermal cells.

Bulliform cells.—The bulliform cells are similar in size to those found in Lolium perenne. They are five in number, three large cells in center and one smaller one on either side. These are much more strongly developed toward the middle of leaf than on the margin. On approaching the margin of the leaf the bulliform cells can hardly be distinguished from ordinary epidermal cells.

Mestome bundles.—The number of mestome bundles in a single cross section in middle of leaf is twenty-four, and are not so close as in Lolium. There are three types. First, primary type, open on inferior and superior sides. Secondary type, those that are entirely closed, and these are most numerous. Third, the intermediate type, which are open only on superior side. The bundles of secondary type are most numerous. Three of the closed bundles occur near the margin of leaf. One bundle of the primary type is found next to the closed bundles. The third type is found to the left of mestome bundle of carene, and to the right of carene is found a mestome bundle of second type. One primary mestome bundle occurs in carene.

In the carene leptome and hadrome are well developed. The pitted vessels are large. Stereome is well developed on inferior
and superior surfaces of the bundle. In the carene, leptome and hadrome are separated from each other by thick-walled cells. The cells in leptome are somewhat more thick-walled than in hadrome.

In some of the mestome bundles of third type the hadrome is not so well developed; the intercellular space is not evident. This is not the case with mestome bundles of first type, in which this space is very conspicuous. The leptome is in direct contact with stereome, but hadrome is separated by thin-walled parenchyma cells. The bundles of second type are small; leptome and hadrome are but slightly developed, most of the bundles containing only thick-walled cells, while occasionally there is a bundle which has an indication of one or two pitted vessels. In the mestome bundle of third type, the leptome is separated from the stereome by thin-walled parenchyma cells.

In Festuca elatior var. pratensis, as in Lolium perenne, a thin-walled parenchyma sheath surrounds all bundles of the second type, but in all cases thick-walled cells form a closed sheath around leptome and hadrome just inside of parenchyma sheath.

Stereome.—This consists usually of six cells at the margins of leaf and occurs on superior surfaces of all bundles of the first and third types, and occasionally on superior surface of the mestome bundles of second type. It is not, however, strongly developed. Greatest development is reached on superior and inferior surfaces of mestome bundles of carene.

Mesophyll.—This is found between all mestome bundles. The mestome bundles are found not so close as in Lolium perenne. The cells are smaller. The smaller occur on superior face. The epidermal cells of stereome region are thick-walled.

FESTUCA TENELLA WILDL.  
(Pl. ix, Fig. 2; Pl. x, Figs. 5 and 6.)

Epidermis.—The epidermis is as strongly developed as in Festuca elatior var. pratensis though not as large as in Lolium. The smaller cells occur on superior surface. The cuticle is thicker on inferior surface than on superior surface. The epidermal cells covering the stereome are thick-walled and not as large as the other epidermal cells.

This dry soil grass has involute leaves and, as Hackel says: "In grasses that do not have such fan-shaped cell groups (bulliform cells) the blade remains always folded or rolled up, or at least open but a little." Bulliform cells do not occur, or only as slight differentiation of epidermal cells.
Trichomes are conspicuous, but only on the superior surface, one to three to each bundle.

_Mestome bundles._—There are twelve mestome bundles in a leaf, of three types. First, primary type, open both on inferior and superior surfaces of leaf, _i.e._, those which have hadrome and leptome respectively in contact with stereome, either in direct contact or are separated from it by several rows of thin-walled parenchyma cells. Second, the secondary type. These are entirely surrounded by chlorophyll-bearing parenchyma. Third, intermediate type. These open inferiorly. Only one bundle of primary type occurs and this is in the carene. The leptome and hadrome are in direct contact with each other. The leptome is separated from the stereome by thin-walled parenchyma cells. Quite a development of thin-walled parenchyma cells occurs above the mestome bundles of carene. Two bundles of the third type occur near the margin of leaf. The cells separating the leptome from stereome are in this case somewhat thicker-walled than those in carene.

The mestome bundles of second type are of two sizes, the largest ones having leptome and hadrome poorly developed, and the smallest having no thick-walled cells.

The thin-walled parenchyma, with its inner closed sheath does not differ from that described in _Festuca pratensis_ and _Lolium perenne._

_Stereome._—This seems to be more strongly developed in this species than in _Festuca elatior_, variety _pratensis_ and _Lolium perenne_. It occurs on the margin of leaf, and also on inferior surface of all bundles of first and third types, and on inferior surface of all large bundles of secondary type.

_Mesophyll_ occupies a small area in this species since the mestome bundles are close together.

**BROMUS PATULUS M. & K.**

_(Pl. ix, Fig. 4; Pl. x, Fig. 7.)_

This was thought to be _B. racemosus._

_Epidermis._—The large epidermal cells are thicker-walled than in _Festuca_ or _Lolium perenne_—Over the stereome they are smaller and thicker-walled. The cuticle is thicker on superior than on inferior surface. The leaves are very hairy, and trichomes occur both on inferior and on superior surface, but are more numerous on superior surface.
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Bulliform cells.—The bulliform cells are not greatly differentiated. In a great many cases the cells are hardly to be distinguished from epidermal cells proper. They occur between each mestome bundle and number three.

In the middle of the leaf there are from thirty to thirty-three mestome bundles of three types: primary, secondary and intermediate.

The mestome bundles of secondary type are most numerous, sixteen in each leaf. These bundles are rather small, and occur near the margin of the leaf. Those of the secondary type consist mainly of thick-walled cells with poorly developed pitted vessels. One mestome bundle of second type occurs on each side of mestome bundle of carene.

Three sizes of mestome bundle of first type occur. One is found in the carene. This is the largest; other sizes follow in numerical order, beginning from margin. The smallest is shown in plate IX.

In the two larger, the leptome and hadrome is well developed, and in the smallest bundle the spiral duct in some instances is wanting.

Stereome.—This is quite conspicuous in the carene. Hadrome separated from stereome by colorless parenchyma cells. In carene the stereome is more strongly developed on inferior than on superior surface of mestome bundles. The mestome bundle of second size has the stereome not so well developed on its superior and inferior surfaces as is found in carene. The mestome bundle of third type is of the same size as the smallest of the first type, only they are more numerous.

Stereome is found on the margin of leaf, and numbers from four to six cells; it also occurs on superior and inferior surfaces of all bundles, except those of the second type. It does not occur on either superior or inferior surface of the bundles of second type.

Mesophyll.—This occurs between all mestome bundles. The cells are quite uniform in size.

EXPLANATION OF PLATES.

All drawings were made with the camera, and are drawn to the same scale. The abbreviations used are: C., cuticle; E., epidermis; E. C., epidermal cells; Sto., stoma; Tr., trichomes; B., bulliform cells; Ste., stereome; Mes., mesophyll; C. B. P., chlorophyll-bearing parenchyma; Car., carene; M., mestome bundles; H., hadrome; L., leptome.

Plate IX, Fig. 1. Festuca elatior, var. pratensis. Fig. 2, Festuca tenella; Fig. 3, Lolium perenne; Fig. 4, Bromus patulus.

Plate X, Figs. 5 and 6, Festuca tenella; Fig. 7, Bromus patulus.

Plate XI, Fig. 8, Lolium perenne; Fig. 9, Festuca elatior, var. pratensis.