SHORT COMMUNICATIONS

ALEURONE TRANSFER CELLS AND OTHER STRUCTURAL FEATURES OF THE SPIKELET OF MILLET*

By S.-Y. Zee†‡ and T. P. O'Brien†

In recent publications we have described the distribution and structure of vascular transfer cells in the floral axes of wheat (Zee and O'Brien 1971) and the presence of a xylem discontinuity composed of modified tracheary elements at the base of the pericarp (Zee and O'Brien 1970*a*). We have also examined the structure of the pigment strand during grain formation (Zee and O'Brien 1970*b*). In order to find out if these structures are present in the florets of a non-festucoid grass we have examined a member of the Paniceae, Japanese millet (*Echinochloa utilis* Ohwi & Yabuno).

Experimental

Samples of mature spikelets of Japanese millet with a small portion of the pedicel still attached were removed from the parent plant and fixed in a mixture of 10% acrolein and 2% glutaraldehyde, dehydrated, and then embedded in glycol methacrylate as described by Feder and O'Brien (1968). Serial longitudinal and transverse sections, 1–2 μm in thickness, were cut using glass knives and examined by light microscopy. Samples of the attachment region between the grain and the pedicel were also dissected out carefully, fixed in 3% glutaraldehyde, and processed for electron microscopy as described by Zee and O'Brien (1971).

Results and Discussion

The spikelet of millet consists of one fertile and one sterile floret, subtended by two unequal glumes, the lower one of which is reduced. At maturity the lemma and palea of the fertile floret are very much hardened and totally enclose the grain.

Figure 1 is a diagram of a sagittal section of the spikelet and shows the distribution of the vascular tissues and transfer cells in the organs of the spikelet. Vascular transfer cells present in the vascular tissues of the pedicel are absent from the traces that supply the glumes, palea, and lemma. The situation in millet therefore differs from that found in wheat where xylem transfer cells are present in all the traces that supply the glumes, palea, and lemmas. Millet differs from wheat in another respect, for only xylem transfer cells are present (Figs. 2 and 3). We have been unable to find phloem transfer cells in any part of the vascular tissues of the millet spikelet.

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† Botany Department, Monash University, Clayton, Vic. 3168. (Address for reprints.)

‡ Present address: Botany Department, University of Hong Kong, Hong Kong.

In wheat and in three other species of grass (ryegrass, oats, and bromegrass) the vascular bundles of the pedicel form a compact cylinder at the base of the pericarp, with xylem forming the core of the cylinder and the phloem encircling it (Zee and

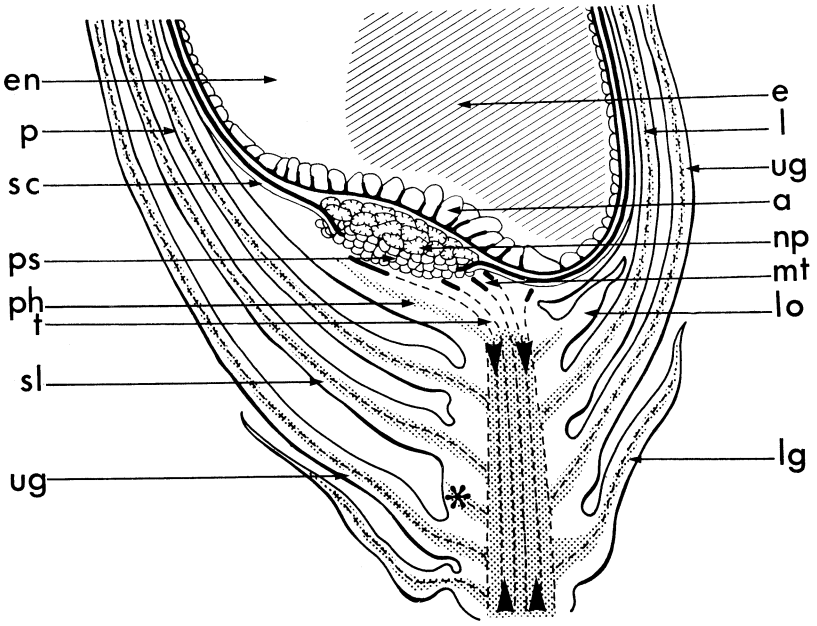

Fig. 1.—A sagittal section of a mature spikelet of millet showing in detail the distribution of the various tissues. *a*, aleurone transfer cell; *e*, embryo; *en*, endosperm; *l*, lemma; *lg*, lower glume; *lo*, lodicule; *mt*, modified tracheary element; *np*, nucellar projection; *p*, palea; *ph*, phloem; *ps*, pigment strand; *sc*, cuticular layer of the seed coat; *sl*, staminate lemma; *t*, tracheary element; *ug*, upper glume. Asterisk denotes position of the vascular remnants of the infertile floret. The region marked by the arrow heads shows the area where xylem transfer cells occur. Note that the aleurone transfer cells (*a*) are restricted to the "gap" in the seed coat.

O'Brien 1970*a*). In millet, phloem and xylem separate from one another, the xylem consisting of a number of minute strands of tracheary elements that terminate in a short length of unlignified tracheary elements, which may be similar structurally to the modified tracheary elements at the base of the pericarp in wheat (Zee and O'Brien

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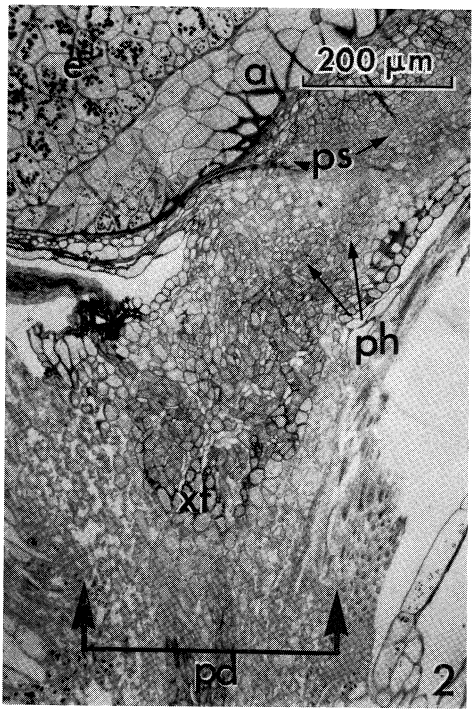
Fig. 2.—A low magnification view of the region between the grain and the pedicel (*pd*) seen in longitudinal section. *a*, aleurone transfer cell; *e*, endosperm; *ph*, phloem; *ps*, pigment strand; *xt*, xylem transfer cell.

Fig. 3.—A high magnification view of the xylem transfer cells (*xt*) in the pedicel seen in oblique longitudinal section. *t*, tracheary element.

Fig. 4.—An oblique transverse section through the pad of tissue at the bottom of the ovary. *a*, aleurone transfer cell; *mt*, modified tracheary elements; *np*, nucellar projection; *ps*, pigment strand.

Fig. 5.—A higher magnification view of the aleurone transfer cell (*a*). *np*, nucellar projection.

Fig. 6.—An electron micrograph showing the walls (*w*) of the aleurone transfer cell in greater detail. Glutaraldehyde fixation.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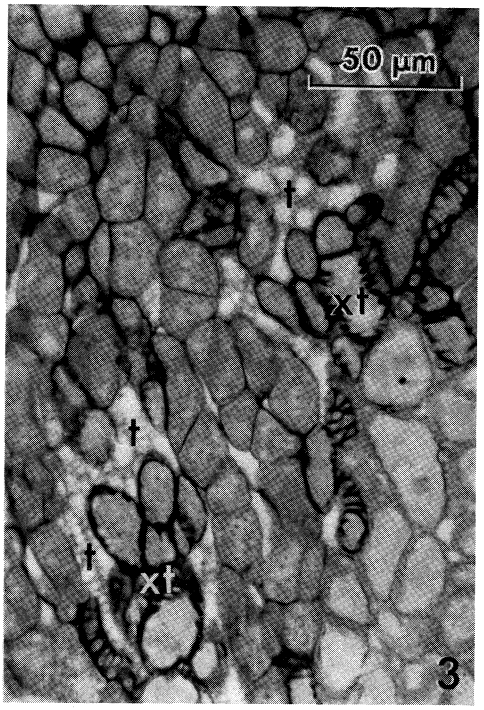
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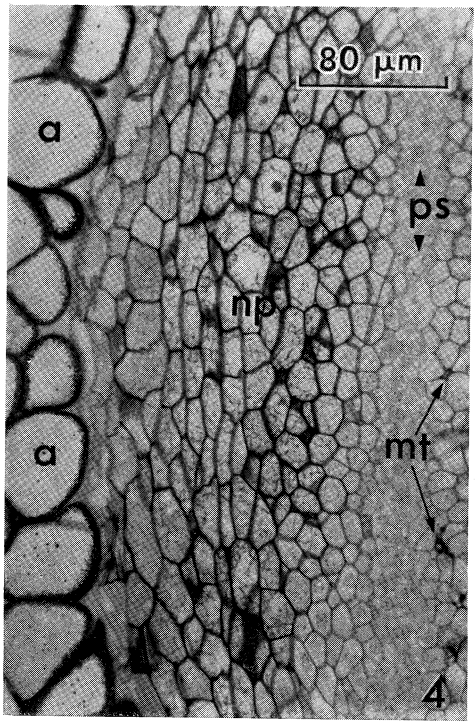
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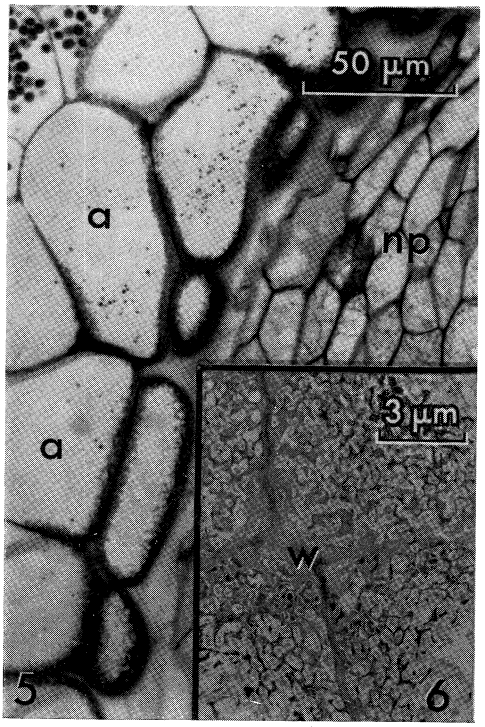
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6

1970*a*). The phloem, consisting of a few strands of sieve elements and associated parenchyma cells, lies on the side of pericarp tissue further removed from the ovule.

In millet the chalazal tissue, from which the integuments develop, is restricted to a small zone at the base of the ovary. A core of cells with lignified walls and suberized contents forms within this chalazal tissue. The cells of this layer appear to be very similar to those of the pigment strand in wheat. Since we have discussed the structure and possible functions of this layer in wheat in detail (Zee and O'Brien 1970*b*) it is sufficient here just to note that a similar layer is present in the "gap" of the seed coat in millet.

The cells of the nucellar projection that lie between the pigment strand and the cells of the aleurone layer at the base of the endosperm are also of interest. In the mature spikelets studied here these cells appear to possess labyrinthine wall ingrowths when viewed with the light microscope (Figs. 4 and 5). However, in the electron microscope these "ingrowths" are rather badly disorganized and it is possible that they represent layers of wall material that have been sloughed off. Only an ontogenetic study of these cells can determine whether this is the case or whether these nucellar projection cells are yet another example of a transfer cell.

However, there is no doubt that the cells of the aleurone layer that lie opposite the nucellar projection have well developed wall ingrowths characteristic of transfer cells (Figs. 1, 4, 5, and 6). Similar cells have been illustrated in corn by Kiesselbach and Walker (1952) and described in yellow foxtail grass (*Setaria lutescens*) by Rost (1970) and Rost and Lersten (1971). In all of these cases the region of nutrient entry to the developing embryo and endosperm is restricted to the small gap in the seed coats that lies at the base of the ovary. The corresponding gap in the seed coat of wheat is considerably extended along the groove of the grain, and the aleurone cells do not have wall ingrowths. It seems likely that in the species with a small gap in the seed coats this region represents a "structural bottleneck" and that the modification of the cells of the aleurone layer (and perhaps those of the nucellar projection) in that region is a device to aid the entry of solutes into the ovary.

Concluding Remarks

The differences between the distribution of transfer cells in wheat and millet seem to underscore our ignorance of the mechanisms by which nutrients from the parent plant are transferred to developing embryos and endosperm. Gunning and Pate (1969) suggest that transfer cells develop in any anatomical situation where "adverse surface area–volume relationships exist between donor and receptor compartments of the transport pathway and/or where the transported solutes are accompanied by minimal flow of solvent". It seems reasonable to equate the presence of transfer cells in the aleurone layer at the base of the ovaries of *Zea*, *Setaria*, and *Echinochloa* with the small gap in the seed coat in these plants. However, how is one to explain the total absence of phloem transfer cells, and the absence of xylem transfer cells from the lower parts of the traces of the sterile glumes, palea, and lemmas in millet when the same regions are richly supplied with xylem transfer cells in wheat? Do glumes contribute less nutrient to grain formation in millet than in wheat? One cannot help but feel that we shall not come to understand the significance of the distribution of transfer cells in different situations until we know a great deal more about the metabolic activities of these cells.

Acknowledgments

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