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Anatomical Study of Seed Shattering in Bahiagrass and Dallisgrass

Byron L. Burson, Jario Correa, and Howard C. Potts

ABSTRACT

Seed shattering is a major problem in ‘Pensacola’ bahiagrass (Paspalum notatum Flugge) and dallisgrass (P. dilatatum Poir.) which often reduces availability and quality of seed of these species. An anatomical investigation of the abscission layer formation in the pedicel of Pensacola bahiagrass, common dallisgrass, and yellow-anthered dallisgrass was conducted to determine the sequential histogenesis of the layer, and to relate its development to different morphological stages of the developing inflorescences for each species. The abscission layer was located in the pedicel just below the glumes in each species. In bahiagrass it became distinguishable while the inflorescence was in the boot stage, and by anthesis it was fully developed. The layer appeared as a ribbon of thick walled cells, five to seven cells wide, extending across the pedicel. Eight to 10 days after anthesis the abscission cells elongated and collapsed. Small lacunae were initiated adjacent to the vascular strands and continued to increase in size until the crushed vascular and pith cells had completely disintegrated. Spikelets remained attached to the pedicels by the epidermal cells until abscission occurred approximately 15 days after anthesis.

In both dallisgrass biotypes the layer became distinguishable when the inflorescence was intermediate between early boot and boot stages, and was fully developed by anthesis. The layer appeared as a slightly wedge-shaped band of thick walled cells, six cells wide at the epidermal edge and four cells wide at the vascular bundles, extending across the pedicel. Six days after anthesis, abscission layer cells in yellow-anthered dallisgrass became elongated, and 9 days after anthesis a similar behavior was observed in common dallisgrass. In both biotypes, cells in the layer collapsed, leaving a crushed mass of cells. This and the remaining events were similar to those observed in bahiagrass. Abscission occurred on the 15th day after anthesis in the yellow-anthered biotype, and on the 18th day in common dallisgrass. It appears that the abscission process in these three grasses is primarily biochemical in nature. These findings are probably indicative of the abscission process in other Paspalum species.

Additional index words: Paspalum notatum, P. dilatatum, Histological, Abscission layer.

Seed shattering is common in many Paspalum species including bahiagrass (P. notatum Flugge) and dallisgrass (P. dilatatum Poir.), two of the more economically important grasses in the genus. Both grasses are grown primarily for forage and are propagated by seed. Seed shattering results in reduced seed yields and lowered quality of the harvested seed.

‘Pensacola’ is the most commonly grown cultivar of bahiagrass in the south. Its seeds shatter very badly, often before they mature (4). Correa (6) reported that seed shattering was most severe 14 days after raceme exsertion. He found that 36% of the filled spikelets eventually shattered and concluded that no more than 50% of the spikelets produced could be harvested for seed at any one time.

Poor seed quality is one of the major impediments to the use of common dallisgrass. Seed shattering compounds this problem. Bennett and Marchbanks (2) reported that at least 50% of the spikelets of common dallisgrass shattered 14 days after anthesis. Holt and Bashaw (8) reported that bulk harvested common dallisgrass seed seldom exceeded 20% seed set and could be much below this because of losses from shattering and unfavorable environmental conditions. They found that when individual inflorescences were bagged to avoid the loss of shattered seed, seed set approached 50% under optimum conditions.

Shattering is generally associated with an abscission layer; however, little information is available concerning the mechanisms of shattering in forage grasses. Bonin and Goplen (3) conducted a histological study of seed shattering in reed canarygrass (Phalaris arundinacea L.). They reported that shattering resulted from the disarticulation of the rachilla 12 days after anthesis, followed by the subsequent release of seed from the glumes.

The objectives of this investigation were to determine the sequential development of the abscission layer affecting seed shattering in Pensacola bahiagrass, common dallisgrass, and yellow-anthered dallisgrass, and to relate its development to different morphological stages of the developing inflorescences.

MATERIALS AND METHODS

Material for this study was obtained from 15 plants of each species growing in space-planted nurseries at Mississippi State, Miss., and Temple, Tex. The bahiagrass material was collected during the summers of 1971-73 in Mississippi. Material of both dallisgrass biotypes was collected during the summer of 1975 in Mississippi and 1976 in Texas. Pensacola bahiagrass was established from commercial seed and common dallisgrass from seed of native material. The source of yellow-anthered dallisgrass was PI 235053, a USDA introduction from Uruguay.

Abscission layer formation and development were examined anatomically at six sequential stages of floral development. These were: (a) early boot—shortly after the differentiation of the inflorescence which could not be detected by feeling the leaves enclosing it; (b) boot—the inflorescence could be detected by feeling the leaves enclosing it; (c) initial exsertion—when the inflorescence began to emerge from the leaf sheath; (d) complete exsertion—the inflorescence had completely emerged from the leaf sheath; (e) anthesis—when the anthers began to protrude from the florets; (f) shattering—the initiation of seed shattering. These six stages provided a basis for relating the abscission layer development to a specific morphological stage of plant growth. Since these grasses have indeterminate flowering behavior, it was possible to collect inflorescences at the six different stages of floral development from each plant at the same time throughout the growing season.

The development of the megaspore mother cell and subsequent female gametophyte also was used as a reference in determining
Fig. 1-12. Development and subsequent disintegration of the abscission layer in bahiagrass pedicels. Fig. 1. Spikelet differentiation with no evidence of abscission layer, early boot stage (×160); Fig. 2. Initial formation of abscission layer, boot stage (×110); Fig. 3. Abscission layer clearly defined, late boot stage (×112); Fig. 4. Thickening of cell walls and constriction of vascular strand, initial exsertion stage (×104); Fig. 5. Cells attain maximum size, complete exsertion stage (×115); Fig. 6. Maximum development of abscission zone, anthesis stage (×120); Fig. 7. Interior cells of the abscission layer after cell collapse (×112); Fig. 8. Formation of initial lacunae adjacent to vascular strand 9 days after anthesis (×106); Fig. 9. Lacunae spreading laterally disrupting the vascular strand 10 days after anthesis (×114); Fig. 10. Vascular strand broken 11 days after anthesis (×114); Fig. 11. Coalescence of lacunae 12 days after anthesis (×106); Fig. 12. Abscission layer just prior to seed abscission 13 days after anthesis (×106).
the stage of abscission layer development. This reference was especially helpful at the stages before anthesis. To obtain a clearer understanding of the shattering mechanism, inflorescences were also collected daily from anthesis until 22 days after anthesis.

Inflorescences at the six different stages of floral development were collected from each plant. They were killed and fixed in FAA (90 ml 70% ethanol, 5 ml acetic acid, 5 ml formaldehyde). Approximately 25 spikelets with the pedicels attached were removed from each inflorescence (a minimum of 150 spikelets per plant). They were dehydrated in a tertiary butyl alcohol series, embedded in paraffin, and sectioned with a rotary microtome at a thickness of 15 μm. Spikes at shattering stage were cut at 18 to 20 μm. Mature bahiagrass spikelets were softened with a technique described by Alcorn and Ark (1). The material was stained in the Safranin-0 fast-green series. Microscopic examinations were made on longitudinal sections.

RESULTS

The inflorescence of bahiagrass and dallisgrass is a raceme and the spikelets are attached to the rachis by a pedicel approximately 2.5 mm in length. When seed shattering occurs, the spikelet separates from the pedicel at a point just below the glumes. This portion of the inflorescence was of primary concern in this study.

Bahiagrass. Floret formation was incomplete at the early boot stage; however, the rudimentary lemma, palea, anthers, and ovary of the fertile floret were identifiable. Parenchyma cells in the pedicel region immediately below the spikelet had five to seven sides, and averaged 14 μm in diameter. Some cells had large nuclei, but there was no development of an abscission layer (Fig. 1). As the culm elongated and approached the boot stage, vascular tissue became more evident, and the megaspore mother cell was visible in the ovule.

When the inflorescences reached the boot stage, the abscission layer was clearly evident. Parenchyma cells in the layer were slightly larger, 16 μm in diameter, and had more prominent cell walls than those of the surrounding ground tissue (Fig. 2). Before initial exertion of the inflorescence, the abscission layer was organized into an almost uniform band, five to seven cells in width, extending from the epidermis to the vascular bundles (Fig. 3). The functional megaspore was fully developed at this time.

By initial exertion of the inflorescence, cells in the abscission layer had increased in size to about 20 μm in diameter. Their walls had thickened and a slight constriction of the vascular bundle was evident (Fig. 4). At this stage, a 2- or 4-nucleate embryo sac was present in the ovule. Figures 5 and 6 show the development of the abscission layer at complete exertion and anthesis, respectively. The only apparent differences between these two stages and that of initial exertion were thickening of the cell walls, decrease in cell diameter, and exertion of additional pressure on the vascular tissue. The average cell diameter at complete exertion and anthesis was 18 and 14 μm, respectively.

Approximately 7 to 9 days after anthesis, all interior cells of the abscission layer, including those in the vascular area, had collapsed, leaving what appeared to be a crushed mass of cell walls (Fig. 7). Only a single row of cells typical of those in the abscission layer persisted along each edge of the zone. When originally observed, the crushed cells were assumed to be an artifact resulting from crushing of the tissue by the microtome. However, after sectioning a large number of spikelets oriented at various angles to the microtome blade, it was concluded that collapse of the cells was a normal step in the abscission process.

Figures 8, 9, 10, 11, and 12 represent spikelets collected 9, 10, 11, 12, and 13 days, respectively, after anthesis and illustrate the latter stages of the abscission process. The initial lacunae formed typically in the region adjacent to the vascular bundle (Fig. 8). The lacunae subsequently increased in size by coalescence from the center of the pedicel toward the periphery (Fig. 9-12). The epidermal cells were the last to disintegrate, causing the morphologically mature seed to abscise.

Dallisgrass. At early boot stage, an abscission layer was not evident in either dallisgrass biotype. The parenchyma cells in the pedicel were oblong and had an average dimension of 12 × 21 μm in common dallisgrass and 11 × 18 μm in yellow-anthered dallisgrass.

Abscission layer development began earlier in dallisgrass than in bahiagrass. It was identifiable when the inflorescences were intermediate between the early boot and boot stages. In both biotypes the initial cells were smaller (15 μm diameter), had more prominent cell walls, and were more circular than the surrounding parenchyma cells. The layer began to develop near the epidermis at a time when the megaspore mother cell was visible in the ovule.

After the layer was initiated, it developed rapidly. By the boot stage, the abscission layer was organized into a ribbon of cells extending across the pedicel to the vascular bundle. It was normally five cells wide at the epidermis and three cells wide adjacent to the vascular tissue. The average cell diameter was 15 μm in common dallisgrass and 14 μm in the yellow-anthered biotype. A functional megaspore was present in the ovules of both grasses at this stage.

By initial exertion of the inflorescence, cells in the layer remained essentially the same size as those at the boot stage; however, there was considerable thickening of cell walls and more pressure was exerted against the vascular tissue. In both grasses, the width of the abscission zone had increased to six cells near the outer edge of the pedicel and to four cells adjacent to the vascular bundle, resulting in a wedge-shaped appearance.

In dallisgrass, the florets on the upper racemes of the inflorescence normally initiate anthesis before the lower racemes have completely emerged from the leaf sheath. Thus, there was little anatomical difference in the abscission layer cells (about 14 μm diameter) between the initial exertion and anthesis stages.

In common dallisgrass, the only apparent change during the first 8 days after anthesis was thickening of the cell walls. On the 9th day, the abscission layer cells started elongating and elongation continued until 14 days after anthesis. A darkening of the cytoplasm in the cells intensified with time, and the cells appeared plasmolyzed. Fourteen days after anthesis elongated cells in the layer began to collapse. Prior to collapse, cells had an average size of 8 × 15 μm and many were vacuolated. After collapse, average
cell size was $5 \times 22 \mu m$. On the 18th day, the crushed cells began disintegrating and lacunae began forming near the vascular bundle. Coalescence of the lacunae resulted eventually in spikelet attachment by the epidermal cells only.

Latter stages of layer development and subsequent separation of the pedicel and spikelet in the yellow-anthered biotype were similar to those of common dallisgrass, but the processes occurred earlier in yellow-anthered dallisgrass. Cell elongation was first observed on the 6th day after anthesis. On the 8th day, the cells in the layer began to collapse. The cells were about the same size at this stage as that reported for common dallisgrass. By the 12th day, the crushed cells were disintegrating to form lacunae. Spikelet disarticulation was observed in material collected on the 15th day after anthesis.

DISCUSSION

This investigation revealed that seed shattering in Pensacola bahiagrass, common dallisgrass, and yellow-anthered dallisgrass was conditioned by formation of an abscission layer which extended across the pedicel at the base of the spikelet. Anatomically, the only difference between the dallisgrass biotypes was that the layer separated earlier in the yellow-anthered form than in common. Bahiagrass and dallisgrass differed in stage of layer initiation, cell size, layer shape, and time of disarticulation. However, the basic development of the layer and mechanism of seed disarticulation appeared to be essentially the same anatomically in both species. Due to the similarities in the layer development in these three grasses, we believe these findings can be applied to other Paspalum species.

Two main categories of abscission processes are reported in the literature: (a) disintegration of part or all of the cell wall as a result of biochemical changes and (b) mechanical tearing of the abscission tissue (7). The gradual elongation and eventual collapse of the cells in the layer of the Paspalum species studied suggested the process was biochemical. Apparently, there were physiological changes in the cells within the layer which resulted in their elongation, plasmolysis, and eventual collapse. An enzymatic deterioration of the middle lamella may have been involved in the disruption of the cells with lacunae forming as a result of the deterioration of the collapsed cells.

In the field, initial seed shattering was observed 8 and 15 days after anthesis for yellow-anthered and common dallisgrass, respectively. This was nearly a week earlier than the time of disarticulation observed in the sectioned material. An explanation for this difference could be that after the layer collapsed, the weight of the caryopsis or force of the wind in the field caused the spikelet to shatter early. A majority of the mature spikelets examined anatomically did not contain a caryopsis because the ovule had aborted during development. These spikelets did not have the extra weight of a caryopsis and probably remained attached to the inflorescence longer than those with a caryopsis. Therefore, shattering probably occurs sooner after anthesis than indicated by the anatomical studies. However, these data characterize the layer development in these species.

Plant growth regulators have been used to control the abscission process in plants (5). Most of the work has been limited to horticultural crops. However, in a recent study spikelet abscission in Panicum maximum Jacq. was reduced by 40% when auxin was applied (9). This response was dependent on plant genotype and auxin concentration. It was also determined that gibberellin either stimulated abscission or had no effect. These findings suggest the possibility that the appropriate chemicals, if applied at the correct concentration and stage of development, could delay or prevent abscission layer development in Paspalum species, thus providing a means of controlling seed shattering. As a result of this study the ontogeny of the abscission layer and perhaps time of growth regulator application can be identified by the stage of culm development in the growing plant.

REFERENCES