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Abscission of leaf laminas – An unnoticed factor in tussock grass formation

Martin Röser*, Heike Heklau

Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Neuwerk 21, 06099 Halle, Germany

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ABSTRACT

Drop of leaves at structurally defined abscission zones is a typical feature of dicotyledonous angiosperms. It is rare in monocots including the grass family (Poaceae). Some grass species have an odd, yet poorly studied pattern of leaves disarticulating regularly between the leaf sheath and the leaf lamina. Using species of three distantly related genera, such disarticulation zones were anatomically studied for the first time to clarify the structural background of shedding. The abscission zones of the three species turned out strongly different from each other in position, spatial arrangement and cellular architecture of different tissues, which is described and illustrated in detail. Breakpoints of the lamina were consistently defined by a sharp delineation of parenchymatous against sclerenchymatous tissue, irrespective of how these tissue types were arranged, e.g., sclerenchyma on the top of the sheath (*Danthoniastrum*), at the base of the lamina (*Macrochloa*), or alternating longitudinally with parenchyma (*Aristida*). The tussock grasses *Danthoniastrum* and *Macrochloa* had the most complicated and elaborately structured abscission zones. The results suggest that precise and efficient shedding of leaf laminas is an important factor enabling grasses to form tussocks as implicitly addressed already in 1890 by the agrostologist E. Hackel. Tussocks are a habitually conspicuous and ecologically important growth form of grasses in arid and/or alpine vegetation zones across the world. Judging from our exemplary results it must be expected that even further structural and mechanic patterns of precise leaf blade abscission will be found in tussock grasses of other grass subfamilies, such as the panicoids, chloridoids or arundinoids.

Introduction

A number of plants, particularly trees and shrubs, are deciduous, abscising all of their leaves during a short period. This seasonal abscission is stimulated by several environmental factors such as shortening photoperiod and cold in the temperate zone or drought stress in subtropical and tropical regions. A third pattern is that of vernal leaf abscission, which typically takes place in spring as buds are expanding (Wiesner, 1904).

Leaf abscission is well studied in deciduous dicotyledonous trees and shrubs growing under seasonal climate. They have specialized layers of abscission tissue at the base of the leaf petioles, more rarely within the petiole or in case of pinnate leaves also at the base of the leaflets. These abscission tissues in dicotyledons are weakened by decomposition of middle lamellas between the cells and primary walls induced by plant hormones and leading to the regular drop of leaves from their shoots or leaflets from the rachilla, respectively (Addicott, 1982; Kaussmann and Schiewer, 1989).

In monocotyledons, this type of regular and defined leaf abscission is less frequently encountered (Esau, 1977; Fahn, 1982; Napp-Zinn, 1974). Leaves falling entire as, e.g., in many palms, bamboos, aroids or others do seemingly not always dispose of a highly specialized disarticulation tissue comparable to that of deciduous woody dicotyledons, because leaves seem to drop after withering from time to time and without any defined abscission zone.

A different pattern of abscission is encountered in some grasses: The leaf blades of the basal leaves in flowering and sterile shoots disarticulate from their corresponding leaf sheaths. In morphological terms this means a disarticulation within the leaf and not between the leaf and the shoot. The basal part of the leaves, i.e., the leaf sheaths, is persisting in some of these grasses as a hedgehog-like cushion termed "Stroh-Tunika" (straw tunica) by Hackel (1890). Such persistence of dead and dry basal leaf sheaths leads to the formation of tussocks. Tussock grasses can reach large dimensions (species of *Festuca*, *Helictotrichon*, *Poa*, *Stipa* s.l., etc.) and are typical of dry to arid and high-altitude landscapes. The ecological function of the persistent basal leaf sheath is seen in a sheltering effect against heat and cold or desiccation of the plant and the newly emerging leaves (Hackel, 1890; Hedberg, 1973).

The present study was induced by observations on plants of the Balkanic-Caucasian chasmophytic high mountain grass *Danthoniastrum compactum* collected in the field and cultivated as pot plants for several years in the greenhouses of Halle Botanical Garden. Early in winter all leaves of the basal shoots became yellow and decayed, although temperature was not much lowered in the greenhouses. The leaf blades dropped from their sheaths always

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* Corresponding author. Tel.: +49 5526218; fax: +49 5527094.
E-mail address: martin.roeser@botanik.uni-halle.de (M. Röser).

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at exactly the same position, with the ligule remaining on the top of the sheaths. This was surprising, because the decay of leaves in *Danthoniastrum compactum* was evidently not caused by external factors such as strong wintry cold, which certainly exists in its natural habitat. It was evidently triggered also by an internal, thus inherited growth rhythm, making it a true deciduous grass. This regular seasonal shedding of leaf blades had been unknown for this species, which has likely never been cultivated before, although it had been observed in herbarium specimens that the laminas of *D. compactum* were caducous (Holub, 1980; Watson and Dallwitz, 1992). Judging from our survey of the literature, such growth with an internally triggered seasonal shedding of leaf blades has not yet been reported for any other species of grasses, except eventually *Molinia caerulea* (Salim et al., 1988).

Second, leaf disarticulation with an abscission of the leaf blade is the most obvious and striking physiognomic prerequisite of tussock grass formation, but the anatomical background and the mechanical structure of the break points between blade and sheath has not much been investigated yet (cf. Gordon-Gray and Ward, 1971; Metcalfe, 1960; Napp-Zinn, 1974; Salim et al., 1988). The only comparatively detailed earlier study we found in our survey of the literature was that of Trabut (1889) on *Macrochloa tenacissima* (halfa grass, esparto), whose long and tough leaves were and partly still are harvested in southern Spain and the Maghreb countries for basketwork and the production of paper (Lautensach, 1964; Rikli and Schröter, 1912). The harvesting method used is twisting the upper part of the leaf blade around a stick and then pulling off the leaf blade (Rikli and Schröter, 1912) or reaping the stands.

This induced us to study the anatomy of leaf sheaths and blades and the abscission zone lying in between to obtain some insight into the mechanical background of leaf disarticulation as a fundamental, yet overlooked aspect of tussock grass architecture.

Materials and methods

Plant material and provenances used were *Aristida plumosa* L. (Morocco; Heklau *s.n.*; voucher HAL), *Danthoniastrum compactum* (Boiss. & Heldr.) Holub (Greece, Chelmos; Röser 10688; voucher HAL) and *Macrochloa tenacissima* (L.) Kunth (syn. *Stipa tenacissima* L.; cultivated in Halle Botanical Garden).

Living plant material and dried material rehydrated in commercially available detergent solution and briefly heated in water was used for sectioning (10–15 μm) on a Leica freezing microtome CM 1900. The sections were stained on microscope slides with toluidine blue according to Etzold or safranine/astra blue (Gerlach, 1984). Sections were embedded in synthetic resins Merckoglas (Merck, Darmstadt, Germany) or Phytohistol (Roth, Karlsruhe, Germany). Slides were examined and photographed on a Zeiss Axioskop 2 light microscope.

Results

Danthoniastrum compactum

The disarticulation region of the blade in basal leaves is located precisely at the base of the ca. 1 mm long ligule (Fig. 1b–d). The abscission zone is visible in fresh leaves already externally under low magnification by its pale yellow to brownish instead of green coloration found above and below of it. It is about 30–40 μm long (Fig. 1c). Dry leaves break off from their sheaths quite easily above this pale region.

In longitudinal section, it consists of several layers of comparatively small sclerenchyma cells (Fig. 1h) that are followed above, at the base of the leaf blade, by much larger cells with less strongly thickened cell walls (Fig. 1g). In transverse section this pale yellow zone consists almost entirely of sclerenchyma cells, in which also the vascular bundles are embedded (Fig. 1i). Parenchymatous mesophyll cells with unthickened walls are found only as a thin layer above the abaxial epidermis in the intercostal zones (Fig. 1i).

Transverse sections across the abscission zone of the blade distal to this sclerified region show a lower proportion of sclerenchyma cells. They are arranged around the vascular bundles and connect them to the abaxial epidermis, which has a layer of subepidermal sclerenchyma (Fig. 1g). Mesophyll cells with unthickened walls prevail. These cells collapse or disintegrate in drying leaves, leaving cavities between the bundles. Additionally, the sclerenchyma around the vascular bundles does not reach adaxially up the upper epidermis. It is separated from the adaxial epidermis by parenchymatous tissue and no girders typical of the leaf blade (Fig. 1e) are formed. The cavities left after degeneration of the parenchyma cells and filled by their remnants can be seen also from viewing the top of the leaf sheath after the blade has disarticulated (Fig. 1d).

The leaf blade is comparatively thin and narrow above this abscission zone (Fig. 1d). Astonishingly, it consists in transverse section prevailingly of parenchyma cells, without any girders and only a single-celled layer of abaxial subepidermal sclerenchyma (Fig. 1e). This region misses the prominent longitudinal ribs and furrows occurring on the adaxial surface distally throughout the entire leaf blade (Fig. 1e). The mechanical properties of this thin and weakly sclerified zone, which definitely does not act as the abscission zone, are yet unknown. It functions likely as some kind of flexible joint, transmitting the mechanical impact exerted by wind etc. on the leaf blades down to the actual abscission zone and becomes finally shed with the disarticulating leaf blade.

Macrochloa tenacissima

The disarticulation region of the leaf blades from the sheath is visible in external view by the border of a pale yellow zone at the leaf base sharply delineated against the green upper leaf sheath (Fig. 2b). The base of the leaf blades in transverse section has a thick median abaxial layer (220–270 μm thick) of sclerenchyma fibres, which are up to 140 μm long. The layer extends laterally up to 0.6 mm in width beyond the abaxial leaf epidermis causing the pale yellow colour in external view and is abaxially connected to the bundle sheaths of three vascular bundles (Fig. 2d). The abaxial layer of sclerenchyma fibres decreases in the transition to the leaf sheaths abruptly to ca. 0.15 mm thickness (Fig. 2e and f). The layer additionally is laterally much narrowed and connected to only the median vascular bundle. Only this thin strand extends downwards into the leaf sheath (tangential and transverse sections in Fig. 2e–g) and borders to mesophyll cells. The other sclerenchyma fibres of the leaf base end abruptly at their base with a layer of sclereids, i.e., ± isodiametrical sclerenchyma cells (Fig. 2f and g) that border to mesophyll cells as well. The leaf blades disarticulate at this narrowing below the sclereids (Fig. 2c and g), which is the mechanically obviously weakest zone of the leaf base. After abscission of the blade, a collar looking like a ligule remains on the top of the leaf sheath. This structure, however, is formed by subepidermal mesophyll cells with somewhat thickened cell walls.

Aristida plumosa

The leaves of *Aristida plumosa* show a clear-cut, macroscopically visible external border between leaf sheath and leaf blade (Fig. 3a), but this border does not turn out as the actual abscission zone of the leaf blades. The blades disintegrate slightly above (0.5–1 mm), but without any precisely predictable breaking zone, explaining why variously long basal parts of decayed blades are remaining on the leaf sheaths in this species. Bases of the leaf blades have an abaxial subepidermal layer of thick-walled cells (Fig. 3d with tan-