ANATOMY OF STEM ABSCISSION IN THE GENUS SMILACINA (LILIACEAE)

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Abscission, the shedding of organs or parts, is a phenomenon found in many taxa of both higher and lower plants. The abscission zone associated with the leaves, fruits, and stems of dicotyledons of the Temperate Zone has received much attention, and comparative anatomical studies have been particularly extensive (Lee, 1911; Pfeiffer, 1928; Kozlowski, 1973; Addicott, 1982). An abscission zone typically includes two distinct anatomical regions: a discrete separation layer responsible for the actual detachment of the abscised organ; and a protective layer that seals the parent axis, preventing water loss and the entry of pathogens.

While these two anatomical layers have been found in many dicotyledons, the occurrence of similar layers in monocotyledons is less well known. Separation layers have been found at the leaf insertion of some palms (La Floresta, 1904; Tomlinson, 1962) and in the fronds of the Lemnaceae (Witztum, 1974; Newton *et al.,* 1978). Protective tissues not necessarily associated with the separation of parts occur in many species of monocotyledons. Philipp (1923) classified the protective layers into three types: a metacutis, a simple periderm, and a storied periderm. Philipp, however, was not concerned with the condition or situation in which a plant developed protective layers, and it is unclear when—if ever—these layers are related to abscission.

Stem abscission occurs in many monocotyledons of the Temperate Zone that grow sympodially. Such plants form a stem-abscission zone either at or below ground level as part of their normal seasonal cycle of shoot senescence and shoot regeneration. In this article, the developmental anatomy of abscission is described in *Smilacina racemosa* (L.) Desf. (Liliaceae), a good example of a sympodially regenerating herb with a perennial rhizome. For comparative purposes the abscission scars of four other species in the genus (*Smilacina japonica* A. Gray, *S. stellata* (L.) Desf., *S. scilloidea* Martens & Galeotti, and *S. paniculata* Martens & Galeotti) are examined, although in less detail.

The annual shoot of *Smilacina racemosa* is determinate and consists of a horizontal rhizome and an upright leafy axis. The aerial parts live only a single growing season; they are subsequently replaced by a renewal shoot that develops from a lateral bud found at the base of the leafy axis. The renewal shoot grows horizontally for 2–3 cm before turning upward and forming an overwintering bud that contains the preformed leafy shoot for the following year. This sequence of determinate growth and lateral regeneration is repeated annually.

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Although the aerial portion of each shoot is lost in autumn, the underground part lives for ten or more years; the perennial rhizome is thus a sympodium composed of the persistent basal portions of old shoots. A prominent scar marks the location of each of the abscised parent axes and therefore also the annual growth increment (FIGURE 1).

MATERIALS AND METHODS

The abscission zone in *Smilacina racemosa* was studied in two ways: as it developed without disturbance in local populations at Harvard Forest, Petersham, Massachusetts; and as it developed in response to clipping of the aerial shoot. Previous experience showed that the abscission zone appears naturally during the late summer or fall prior to senescence of the aerial shoot, but developmental studies are difficult because the phenology of individual plants is quite variable. Abscission can be induced in midsummer by cutting the aerial stem just below the lowest leaf, approximately 25 cm above the ground. Such experimentally manipulated plants are advantageous because the abscission zone develops uniformly in them after the aerial stem has been cut.

The aerial shoots of 25 plants within a natural population were cut in this manner on 27 July 1983, and the rhizomes of these plants were subsequently excavated, five at a time, at 0, 3, 7, 14, and 28 days after cutting. Untreated control plants were also collected on each occasion. Additional collections were made throughout the spring, summer, and fall of 1982 and 1983 to extend knowledge of the natural phenology of the protective process.

Fresh material was examined microscopically in transverse and longitudinal hand sections. Additional material was fixed in FAA, dehydrated in TBA, embedded in paraffin, and sectioned at 8 μm. Sections were either stained in safranin and alcian green or subjected to several microchemical tests. The presence of suberin was verified by Sudan IV and the IKI–sulfuric acid test (Johansen, 1940). Lignin was detected by both the HCl–potassium permanganate test (Maule's reagent) according to Johansen (1940) and the HCl-phloroglucinol reaction. In the latter method sections were first dehydrated in eth-

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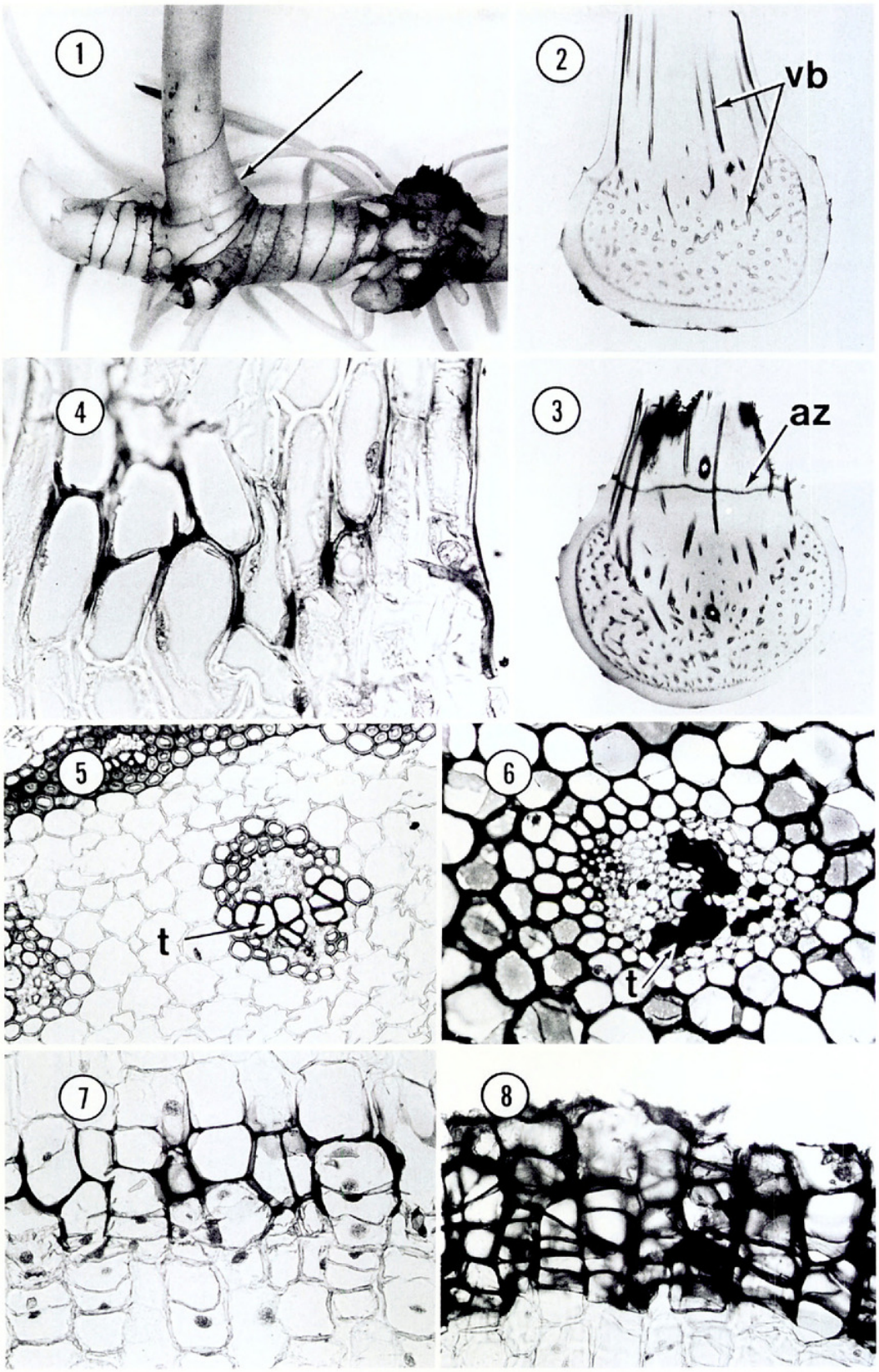
FIGURES 1–8. *Smilacina racemosa*, development of abscission zone. 1–3, 8, untreated control plants; 4–7, abscission induced; all sections stained using HCl-phloroglucinol method. 1, rhizome (August 30), × 0.9; abscission zone visible at base of aerial shoot (arrow), renewal shoot to left, scar of previous year's aerial shoot to right. 2, thick longitudinal section through stem base (June 30), × 1.8, showing vascular bundles (vb). 3, thick longitudinal section through stem base (August 30), × 1.8, showing abscission zone (az). 4, longitudinal section through stem base (7 days after cutting), × 125, showing first stage of abscission; some cell walls lignified. 5, transverse section through stem base at level of abscission zone (7 days after cutting), × 75, showing normal vascular bundle before occlusion of tracheids (t). 6, transverse section through stem base at level of abscission zone (14 days after experimental cutting), × 75, parenchyma cell walls heavily lignified and tracheids (t) occluded. 7, longitudinal section through stem base (14 days



after experimental cutting), × 80, showing newly divided cells proximal to ligno-suberized layer. 8, longitudinal section through stem base (2 years after loss of aerial stem), × 80.

TABLE 1. **Voucher specimens.**

SPECIES	VOUCHER
Smilacina racemosa	U.S.A., Massachusetts, Petersham, *LaFrankie 138.*
S. stellata	U.S.A., Massachusetts, Plum Is., *LaFrankie 76.*
S. japonica	Japan, Yonezawa (material in cultivation at Harvard Forest, Petersham, Massachusetts; no voucher collected).
S. scilloidea	Mexico, Oaxaca, Ixtlán, *LaFrankie IV-21a.*
S. paniculata	Costa Rica, Cerro del Muerte, *LaFrankie IV-10c.*

anol series for complete extraction of soluble sugars and residues of decay, then vacuum infiltrated with 2 percent phloroglucinol in 95 percent ethanol and transferred directly to concentrated hydrochloric acid.

The living and preserved rhizomes of four other species of *Smilacina* were sectioned and stained in a manner similar to that described above. Living plants of these species were not experimentally treated, and development of the abscission zone was not studied directly; however, by examining the successively older scars found within a single rhizome, I could draw some inference concerning the later modification of the abscission zone. Voucher specimens have been deposited in the Gray Herbarium, Harvard University (GH) and are listed in TABLE 1.

RESULTS

SMILACINA RACEMOSA

The parenchyma and vascular bundles at the base of the aerial stem are not distinguishable from the surrounding tissue during the spring and summer (FIGURE 2). As individual stems begin to wither between July and October, a distinct abscission zone forms in the stem base at a scale-leaf internode 1–2 mm above the point of anatomical transition from the rhizome to the aerial stem (FIGURES 1, 3). The rhizome has an endodermis, amphivasal vascular bundles, and isodiametric parenchyma cells; the aerial stem lacks an endodermis but has a peripheral fibrous sheath, collateral vascular bundles, and elongated parenchyma cells. The position and appearance of the abscission zone is the same whether it occurs naturally or is induced.

The abscission zone consists of an outer suberized and lignified layer and an underlying layer of dividing cells that later also become suberized and lignified. The aerial stem usually separates from the rhizome just above the outer lignosuberized tissue, but there is no distinct separation layer, and often the dried stem remains weakly attached for a year or more.

Three stages can be recognized in the development of the abscission zone. In treated plants the first is seen seven days after cutting. (Plants collected zero and three days after cutting show no changes associated with abscission.) In

natural (i.e., untreated) plants this stage usually coincides with the first yellowing of the leaves, but the rate of development varies considerably from plant to plant. In the first stage the primary walls of the cortical parenchyma cells become suberized and partially lignified (FIGURE 4). The development of this ligno-suberized layer spreads inward to the center of the stem and outward until it includes the epidermis. The tracheids of most vascular bundles are water filled in fresh sections and are free of occlusions (FIGURE 5).

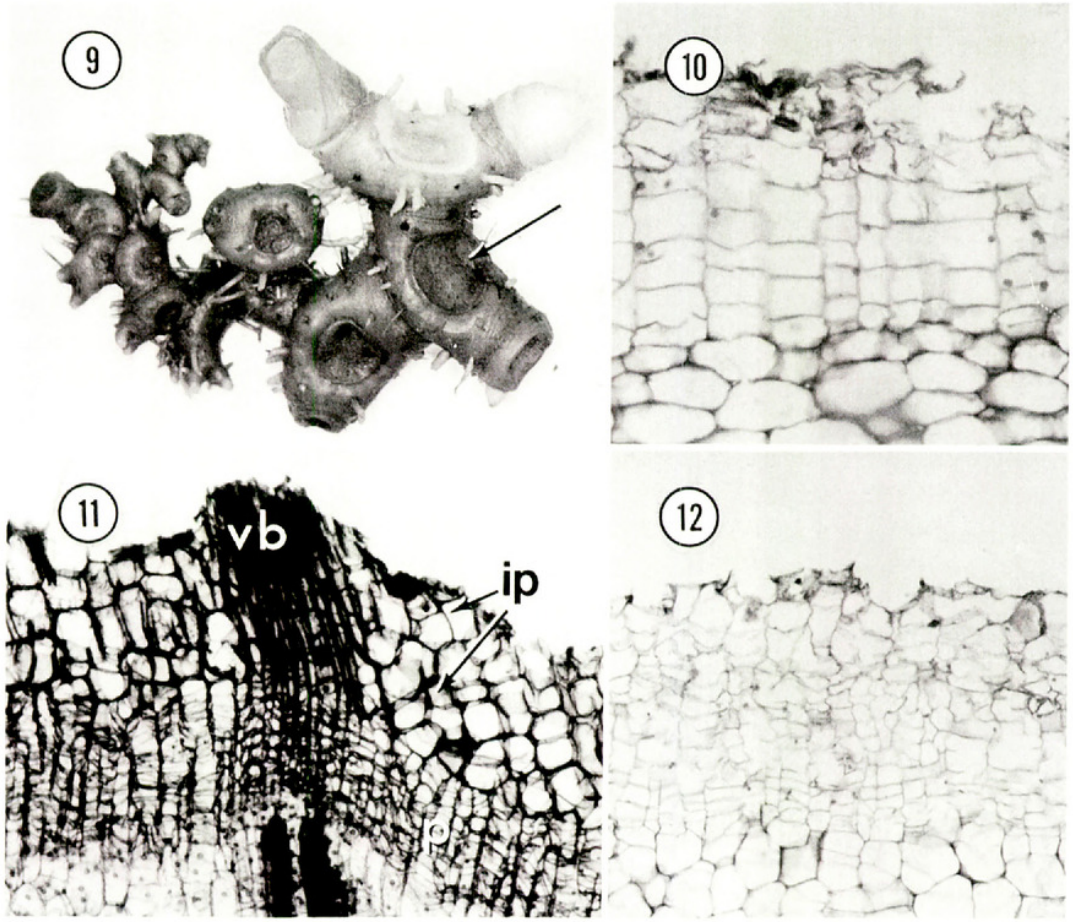
The second stage appears in treated plants 14 days after cutting; in untreated plants it is found when the entire aerial axis has turned yellow or retains only patches of green, and when at least a few leaves have dried and withered. This stage is characterized by an intensified lignin reaction, the occlusion of some of the xylem elements, and divisions within cells proximal to the ligno-suberized layer. The lumens of many tracheary elements are occluded with dark, amorphous contents (FIGURE 6), presumably gums or tannins, while other tracheary elements are air filled when examined in fresh sections. Cells immediately adjacent to the ligno-suberized layer repeatedly divide, with the new cell walls usually forming parallel to the plane of abscission. This results in subdivided cells (FIGURE 7). There is no evidence of a phellogen (i.e., permanently meristematic cells). At this stage the walls of the dividing cells are neither suberized nor lignified.

The third stage in stem abscission is first seen in the experimental plants 21 days after cutting but is found in untreated plants only when the main axis of the aerial shoot is dry and partially collapsed. In this stage the new walls of subdivided cells become suberized and lignified (FIGURE 8). No new cell divisions occur in adjacent cells. Xylem elements are completely occluded in all vascular bundles, and the occlusions extend 2 mm or more into the rhizome. In untreated plants the tissue distal to the ligno-suberized layer may decay, causing the withered aerial shoot to separate from the rhizome. Sometimes the weight of the terminal infructescence breaks the stem adjacent to the protective layer, but no mechanically weakened point or clear separation layer forms. As the aerial axis dries and withers, the ligno-suberized layer and the xylem occlusions become dark red-brown. The development of the protective layer is now complete; no further changes occur with age.

OTHER SPECIES OF SMILACINA

Two other species of *Smilacina* examined (*S. stellata, S. japonica*) have stem-abscission scars anatomically similar to those described for *S. racemosa*. There is a ligno-suberized layer of undivided and divided cells, beneath which occurs seemingly normal parenchyma.

Smilacina paniculata, an herb from montane cloud forests in Costa Rica, differs from the other species studied in the greater width of its aerial stem, and in that the rhizome of the renewal shoot swells to several times its initial diameter soon after the aerial axis emerges (FIGURE 9). Consequently, the abscission scar in *S. paniculata* is much larger than that found in any of the other species. The rhizome of *S. paniculata* is also distinct in that the epidermis is lost during the initial expansion of the rhizome, and a simple periderm subsequently develops on all of the exposed rhizome surfaces (FIGURE 10).



FIGURES 9–12. *Smilacina paniculata*, rhizome morphology and longitudinal sections. 9, rhizome viewed from above, × 0.2, showing scars of old shoots (arrow). 10, periderm of free rhizome surface, stained in safranin and alcian green, × 120. 11, stem base ca. 2 years after abscission of aerial shoot, stained in HCl-phloroglucinol, × 40; initial protective layer (ip) above, vascular bundle (vb) ruptured by periderm (p). 12, lower region of abscission zone, × 120, showing dividing parenchyma cells adjacent to periderm, × 100.

When the abscission zone of *Smilacina paniculata* first develops at the base of the aerial shoot, it is similar to that described for *S. racemosa* (i.e., a ligno-suberized layer of two or three cells). A few cell divisions occur in the parenchyma on the rhizome side of the ligno-suberized layer, and the resulting cells are subsequently incorporated into the protective layer. The tracheids of the vascular bundles are occluded several millimeters into the rhizome. These features characterize the protective region for approximately one year after the loss of the aerial shoot. In older portions of the rhizome, a thick periderm develops beneath the ligno-suberized layer (FIGURE 11), transecting the vascular bundles and augmenting the protective tissue of the abscission scar. The periderm of the abscission region joins with that of the free rhizome surface, but the two types of periderm can be distinguished by structural differences.

The periderm of the free rhizome surface consists of radial files of six or

seven cells that are uniform in size and shape, suggesting that they are derivatives of a phellogen, although this phellogen appears not to be permanent. When mature, all of the cells of the periderm are fully suberized and lignified and are quite distinct from the adjacent parenchyma. No cells occur in intermediate stages of development, which indicates that the periderm is not augmented through the continuous generation of new cells.

The periderm of the abscission region is thicker than that of the rhizome surface, it is not clearly demarcated from the adjacent parenchyma, and there is no indication of a phellogen. The mature periderm cells are varied in size and shape (FIGURE 12). Cell divisions seem to occur in parenchyma cells of progressively deeper levels, so that even when most of the periderm cells are suberized and lignified, parenchyma cells to the interior can be found dividing. Consequently, no clear line separates the periderm from the otherwise normal rhizome parenchyma.

The other tropical species examined, *Smilacina scilloidea,* is similar to *S. racemosa* and *S. stellata* in general morphology, but it develops a periderm on its free rhizome surface and in the abscission-scar region; the periderm is anatomically similar to that found in *S. paniculata.*

DISCUSSION

The abscission zone of *Smilacina* consists only of a protective layer that seals the parent stem; no discrete separation layer is formed. Such a situation may be characteristic of geophytes with sympodial rhizomes, but this generality can be supported only if many more species are examined.

The protective layer that seals the rhizome in *Smilacina racemosa* is notable for its early development, for the limited number of cells involved, and for its durability. In all but the last respect, the protective layer is similar to that found in the leaf-abscission zone of herbaceous dicotyledons. In plants such as *Phaseolus* and *Gossypium,* the initial protective layer forms when the cell walls of three or four layers of cells on the stem side of the separation layer become suberized and lignified. Tyloses occlude the vascular elements, and a few cell divisions occur adjacent to the ligno-suberized layer (Gawadi & Avery, 1950; Lee, 1911). Lee (1911) called these tissues the "initial protective layer" to distinguish them from a secondary protective layer that develops from a phellogen. It is quite remarkable that in *S. racemosa* such an initial protective region is able to seal the rhizome and remain intact for many years or even decades.

Many woody dicotyledons augment the initial protective layer with a periderm that develops some distance to the stem side of the abscission zone. Lee (1911) described the various ways in which this can occur, but typically a phellogen develops below the initial protective layer and establishes continuity with the periderm of the parent stem. In *Smilacina paniculata* the initial protective region is likewise augmented by a periderm, but a phellogen does not develop. Rather, the periderm is derived through the periclinal (and occasionally anticlinal) divisions of subjacent cells, and in this respect it more closely resembles the wound tissue of monocotyledons described by Swamy

and Sivaramakrishna (1972) than it does either the periderm found in the rhizome surface or the periderm described for other monocotyledons (Philipp, 1923). Admittedly, periderm tissue is poorly known in monocotyledons, and a better appreciation of the relationship of wound tissue to periderm tissue awaits their more careful comparative analysis. The protective region described for *Smilacina* can best be considered as an anticipatory wound response, establishing a water-tight seal prior to an actual break in the aerial axis.

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