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Abscission Zone Anatomy, Development, and Separation in *Nicotiana tabacum*

By Robert E. Yager

Abstract. Anatomical differences between Lizard's Tail and Little Turkish varieties of *Nicotiana tabacum* which exist during development of the separation zone and as floral abscission occurs are described. Cells are larger in Little Turkish by an average of 5 to 6 microns in the abscission zone and by 10 microns in the developing fruit. The separation layer in Little Turkish is located 5 to 7 tiers of cells distal to the groove and is usually composed of only 4 to 6 tiers. In Lizard's Tail the separation layer is 8 to 12 tiers distal to the groove, and as many as 50 tiers of cells may be involved. Although there is a seasonal variation in the time required for the completion of the separation reactions, the process involves several additional days in Little Turkish. In both varieties abscission seems to occur as a result of the dissolution of the middle lamella. The cellulose walls appear to be unchanged after the completion of abscission.

A wide variation in the Lizard's Tail and Little Turkish varieties of *Nicotiana tabacum* was reported by Paleg in 1955. Differences in flower structure, growing habits, gross anatomy, means of pollination, and time of abscission were observed. Yager and Muir (1958*a*, 1958*b*) have also reported differences between the two varieties concerning the regulation of abscission by methionine and indoleacetic acid. The effects of various pectic enzymes in the control of abscission are further examples of physiologic differences (Yager, 1959). In this investigation special attention was directed to variations in the development of the separation zone and the occurrence of abscission when fertilization did not occur.

Characteristics of the Mature Pedicel

The separation zone is located at the base of the pedicel in both Little Turkish and Lizard's Tail varieties of *Nicotiana tabacum*. A groove marks the proximal portion of the separation zone, as illustrated in Figures 1 and 2. The vascular system of the mature pedicel is composed of intraxylary phloem and a continuous ring of tracheae. The pith and cortex consist of parenchyma cells which are isodiametric in the case of the pith but are two to three times longer than wide in the case of the cortex. Mechanical tissue is absent in the pedicel until fertilization occurs. At this time walls of cells of the vascular strand display increased thickenings. Kendall (1918) reported these to be wood fibers. The epidermis is typical. The cuticle is poorly developed in the pedicel, especially in the region of the groove (Figures 1 and 2). The smallest cells are found in the center of the region and increase in size on either side of the zone until the usual size of the cortical and pith cells is reached. This

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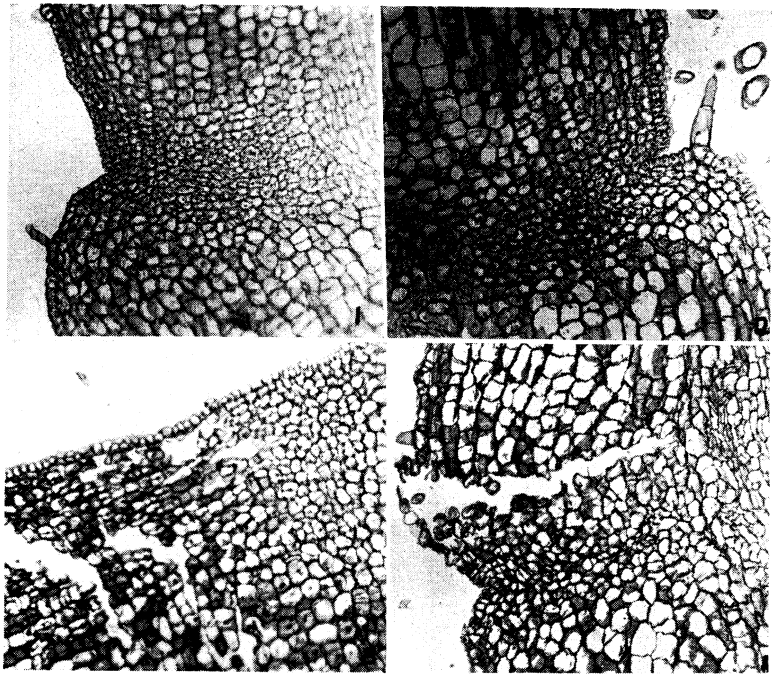

Figure 1. Longitudinal section through the adaxial side of the abscission zone of the pedicel of Lizard's Tail tobacco when flower is at anthesis. (X120)

Figure 2. Longitudinal section through the adaxial side of the abscission zone of the pedicel of Little Turkish tobacco when flower is at anthesis. (X120)

Figure 3. Longitudinal section through the abaxial side of the abscission zone of the pedicel of Lizard's Tail tobacco illustrating separation of cells during abscission. (X120)

Figure 4. Longitudinal section through the adaxial side of the abscission zone of the pedicel of Little Turkish tobacco illustrating separation of cells during abscission. (X120)

band of cells is about 12 tiers of cells thick on the adaxial side of the pedicel and slightly thicker on the abaxial side. The separation layer (where actual separation occurs) is located 5 to 7 tiers of cells distal to the groove in Little Turkish (Figure 4). In Lizard's Tail this distance is about 8 to 12 tiers distal to the groove (Figure 3).

The cells of the separation layer do not appear to be morphologically differentiated in any way from the others cells of the zone in either variety (Figures 1 and 2) when the flower is at anthesis. From microscopic examination it would appear that any cell of the zone could function as a separation cell. Careful study indicates that the separation cells are slightly smaller than surrounding cortical and pith cells, especially those immediately distal to the zone.

There is a marked increase in the size of the pedicel during the development of fruit, especially in Little Turkish. The pith changes only slightly; the major increase occurs in the cortex. The growth is due to cell enlargement rather than division. Cortical cells in the pedicel of the flower of Little Turkish are approximately 18 microns

in diameter, whereas corresponding cells in the pedicel of the developing fruit are approximately 35 microns in diameter. In Lizard's Tail the cortical cells of the pedicels are only slightly smaller in the flower and increase to approximately 25 microns in the fruit (Figures 5 and 6).

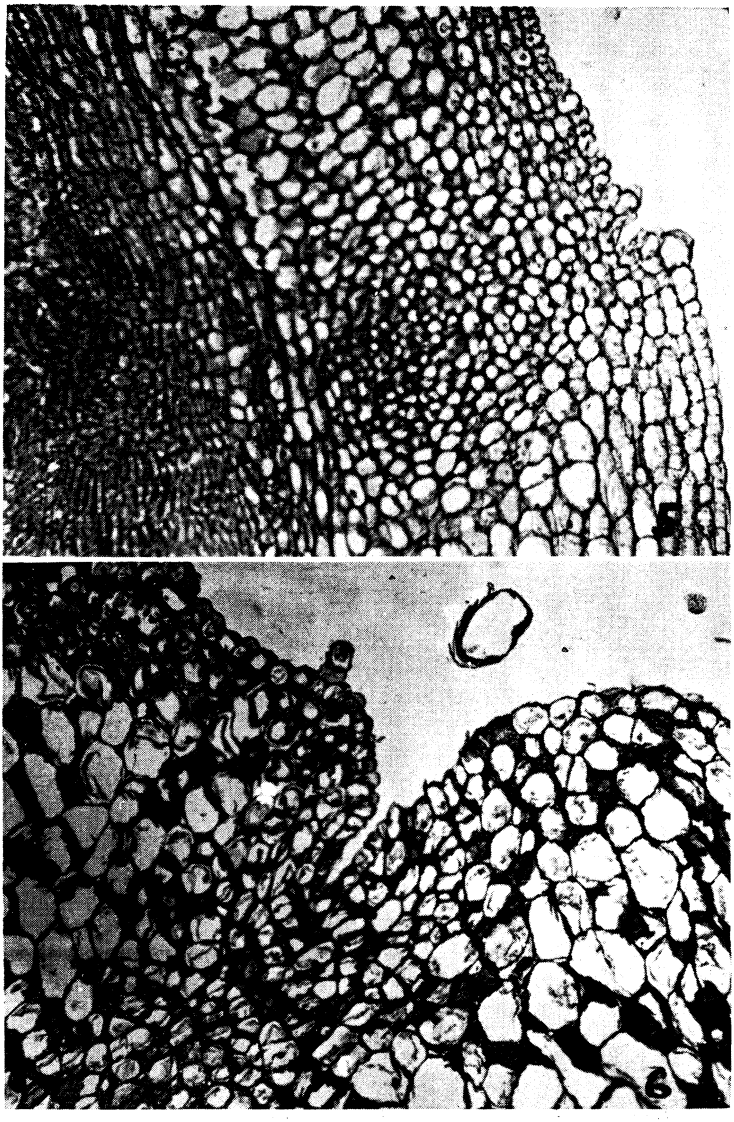

Figure 5. Longitudinal section through the abaxial side of the abscission zone of the pedicel of Lizard's Tail tobacco two weeks following fertilization. (X200)

Figure 6. Longitudinal section through the adaxial side of the abscission zone of the pedicel of Little Turkish tobacco two weeks following fertilization. (X200)

The increase in size is also caused by division of the cambium cells. There is an average of 6 cells between the xylem and phloem in the flower. In the developing fruit this is nearly doubled in both varieties.

The wood fibers begin to form slightly less than a week following anthesis. Fiber formation is much more apparent in Little Turkish than it is in Lizard's Tail, but in each case the tissue develops on both sides of the separation zone before becoming continuous through the zone.

Development of the Separation Zone

The separation zone (region of smaller cells) cannot be observed in young buds which are 2 or 3 millimeters or less in length. The groove begins to form soon after the bud has reached the 2 to 3 millimeter size and appears first on the adaxial side of the young pedicel. Groove formation is more extreme in the case of Little Turkish. The cells in the zone fail to enlarge as do the surrounding cells as the flower matures.

In these early stages the size of the cortical region is proportionately smaller as compared to the cortex in the mature pedicel. This is not true of the pith. It would appear, therefore, that the cells of the separation zone are smaller because they retain their original size while the rest of the cortical cells increase in size. The fact that the groove forms suggests that there are fewer cell divisions, or none, in the cortical part of the zone during the development of the bud. Division of cells on either side of the groove results in an increased diameter of the pedicel, thus explaining the formation of the groove where there is no similar increase in diameter. The cells of the zone in the pith retain their meristematic activity for some time.

The region of small cells is not directly related to the regulation of abscission. In the first place, young buds often abscise naturally or can be induced to do so before the groove and separation zone are differentiated. Secondly, the actual separation layer is located several tiers of cells distal to this region.

The Process of Abscission

The process of cell separation begins on the adaxial side of the pedicel as seen in Figure 4. Cells of the cortex a short distance distal to the groove begin to separate. This separation then spreads to the abaxial side of the pedicel. At times there seems to be an external bulging of the epidermis preceding the separation of it. The dissolution appears to start simultaneously in the pith.

There is a great difference in the dissolution exemplified by Little Turkish and by Lizard's Tail. In Lizard's Tail there are many tiers

of cells involved in the process. In a plant grown in an enclosure where mechanical disturbance is at a minimum, as many as 50 tiers of cells may be involved in the separation layer of Lizard's Tail, but in Little Turkish only 4 to 6 tiers of cells are commonly involved in the dissolution process. In both instances there are fewer tiers of cells involved in the cortical region nearer to the vascular cylinder.

In both Little Turkish and Lizard's Tail the tracheal elements and to some extent the epidermis, which is held together by the cuticle, must be broken mechanically. This factor is more important in Little Turkish because of the greater size of the pedicel and the vascular cylinder.

The regions of separation vary. If the flowers remain on the stem and are kept turgid, the reactions leading to separation develop in a greater number of tiers. The ultimate extent of this development varies considerably in Little Turkish and Lizard's Tail. When the reaction has developed considerably, a white ring formed by isolated masses of cells can be seen on the surface of the pedicel. This is particularly apparent in Lizard's Tail where a ring a millimeter or more wide is common about the base of the pedicel.

No cell division was observed in connection with the separation process. Neither was there any evidence of cellular elongation. The proximal cells after the separation had occurred were longer, but presumably this was the result of increased turgidity caused by decreased pressure from surrounding cells. There was no difference between the two varieties in this respect. Abscission occurs as a result of the dissolution of the middle lamella. The cellulose cell walls appear to be unchanged after the abscission process is completed.

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