THE ANATOMY AND MORPHOLOGY OF THE ABSCISSION LAYER IN TWO CULTIVARS OF *SOLANUM TUBEROSUM* L.[1]

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INTRODUCTION

In connection with a previously reported study (3) on the effects of grafting and/or the use of different understocks, the following observations were made with respect to the abscission layers of potato fruit pedicels or flowers. The objective of the original investigations was to test the effectiveness of grafts or understocks in preventing fruit or flower drop.

Young (4) points out that sheddding of flowers and/or fruits takes place at a definite point. He describes the abscission zone but makes no comparisons among varieties. The present objective was to study the course of development of the abscission layer in the two cultivars and correlate this, if possible, with fruit and seed production.

MATERIALS AND METHODS

Pedicels, from intact flowers, (except in case of abscission) were gathered from greenhouse grown plants. Six stages of development were used as sampling criteria on two potato cultivars: Russet Burbank and Menominee. The stages of development were: small bud, largt bud, open flower, post fruit set, abscissed and small bud just prior to abscission. The difference between the last two stages lies in time of flower or fruit drop. The latter stage has to do with loss of the bud prior to anthesis, while the former involves loss of fruit already set. The small bud stage just prior to abscission was found only in Russet Burbank. It is readily discernible by the yellowing of both the abscission zone and the distal portion of the pedicel beyond.

Pedicel samples, including the abscission zone, were excised, fixed in FAA, and later imbedded using standard procedures (2). The tissue was cut in 12-micron sections and stained with safranin and fast green. Photomicrographs were made from most characteristic slides and comparative studies were made from color prints. Photomicrographs reproduced here in black and white were copied from color prints.

Characteristics common to both varieties were combined into a general physical description of abscission zones of potato flower pedicels. Contrasting characteristics of similarly sampled materials were studied.

RESULTS AND DISCUSSION

In potato flower pedicels the abscission zone layers are not well defined. Abscission zones of Menominee are used as a comparative standard.

The protective layer (1) consists of a large, compact mass of small meristematic cells. These cells are irregular in shape and direction of

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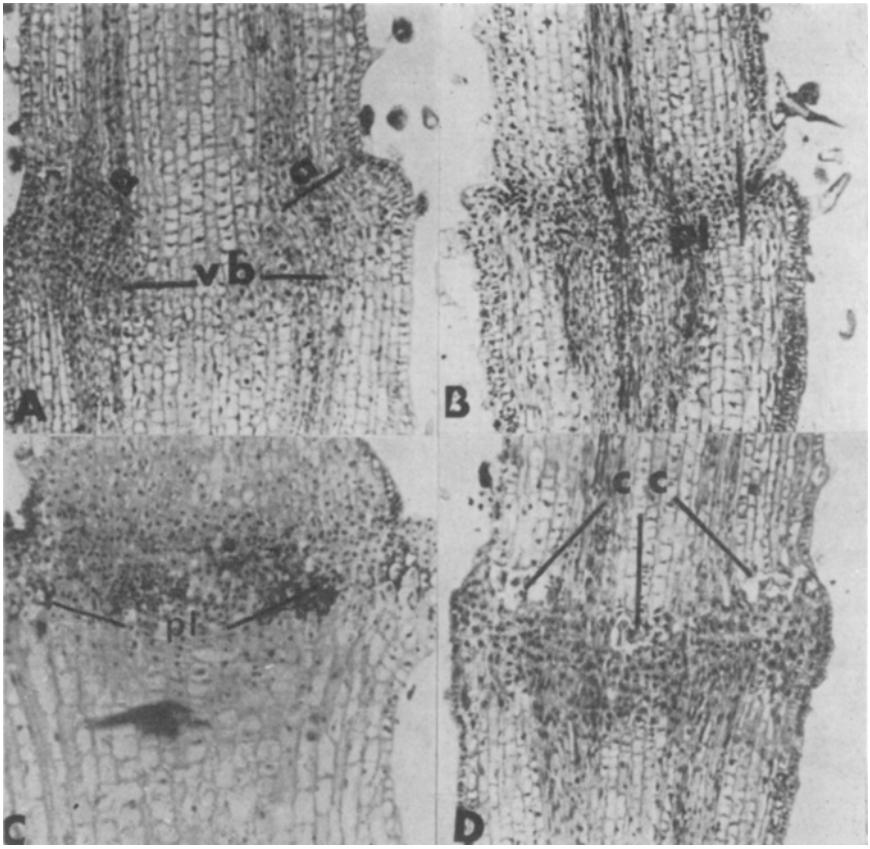

FIG. 1.—A. Menominee, small bud stage; a—area of early development of protective layer, vb—vascular bundles. B. Russet Burbank, small bud stage; pl—protective layer zone. C. Russet Burbank, fruit stage; pl—protective layer zone. D. Russet Burbank, small bud stage just before abscission; cc—area of collapsed cells and separation layer.

division, have large nuclei and dense cytoplasm and occur in a band cutting across the pedicel. It arises when the buds are still small (Fig. 1A). It is first most conspicuous in the fundamental tissues between the epidermis and the vascular tissues (Fig. 1A) and later within the region of vascular tissues (Fig. 1B). Greatest proliferation of meristematic cells, occurs in the immediate area of the vascular system (Fig. 2A). The layer is crescent shaped, narrow at the tips, and wider toward the middle. Viewed from the top, it would have a bowl-shaped appearance.

In Menominee the protective layer starts to develop at small bud stage (Fig. 1A) and is completed by large bud stage (Fig. 2A). It changes little by fruit stage (Fig. 2D). In Russet Burbank the layer is almost completed by small bud stage (Fig. 1B) and develops very little thereafter (Fig. 1C). Meristematic cells are also smaller and more compact than those of Menominee. The plane of the layer is large and curves

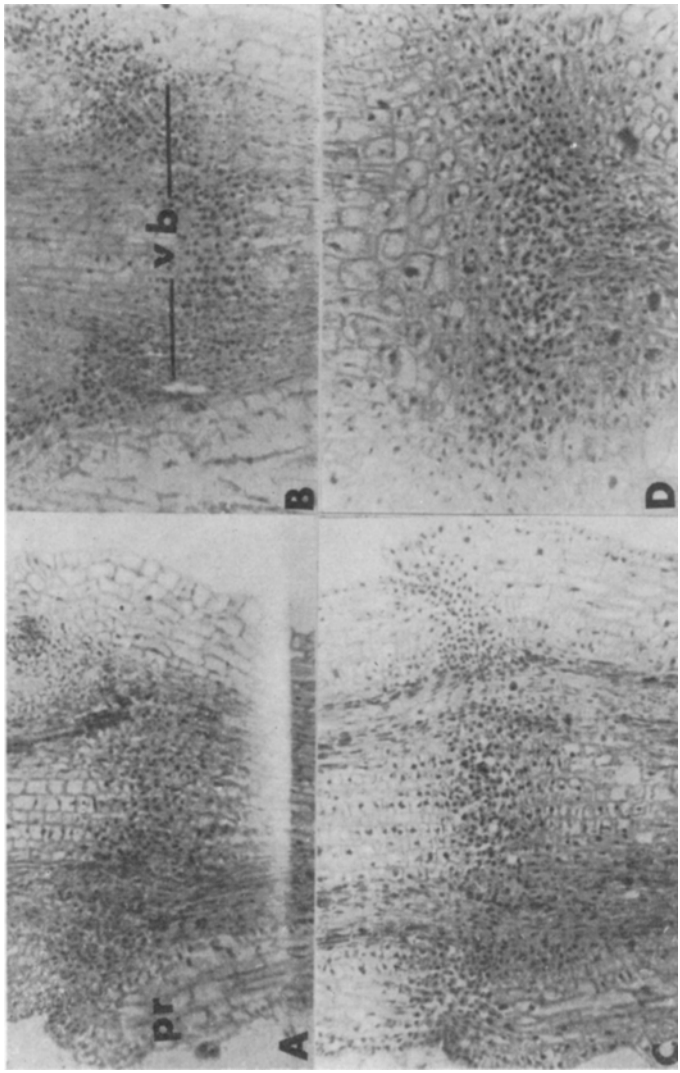

FIG. 2.—A.Menominee, large bud stage; pr—proliferation area.
B. Menominee, open flower stage; vb—vascular bundles.
C. Russet Burbank, open flower stage.
D. Menominee, fruit stage.

strongly downward in Menominee (Fig. 2B), while Russet Burbank has a narrow, almost non-curved protective layer (Figs. 2D & 1C).

There is no visible differentiation of the separation layer in potato flower pedicels. Stages of development just prior to abscission show the separation layer to be bounded proximally by the protective layer and on the periphery by the epidermis. A distal limit (toward the bud) could not be determined. In Russet Burbank the lower boundary of the separation layer is a few cells above the upper limit of the protective layer (Fig. 1D).

The area of separation can readily be determined when the distal

region of the pedicel starts to absciss. Whole regions of cells start to disintegrate and collapse, forming oblong, ragged areas. The collapsed cell walls slightly thicken the boundaries around the perimeters of the disintegrating area. Cell collapse is first detected between the vascular system and the epidermis (Fig. 1D). Later the area within the region of the vascular system breaks down and actual organ drop follows.

There is no disruption of the vascular system prior to actual abscission. In the protective layer the bundles curve outward (Fig. 1A) but otherwise are normal; thus there is no effect on the vascular system by either the protective layer or the abscission layer. No tyloses are seen in the xylem elements either before or following abscission. When the vascular elements are broken at abscission, portions of them often protrude well beyond the protective layer. In Menominee the vascular system within the abscission zone is strongly curved outward (Fig. 2A) while in Russet Burbank this feature is not so conspicuous (Fig. 2C).

Near the top of the protective layer there is an indententation of the pedicel (Fig. 2 A, B, C). Immediately below this is a swelling which is the most characteristic external feature of the abscission zone. This structure is prominent in the small bud stage and arises entirely by enlargement of cells in the area. The affected area extends from the indentation to several cell diameters below the lower limit of the protective layer. There is also evidence of heavier pubescence in this area.

Flower pedicels of Menominee, at all stages, are larger and more robust than those of Russet Burbank. The abscission zone swelling of Russet Burbank is prominent by small bud stage (Fig. 1D) but expands little thereafter. In Menominee the swelling is scarcely noticeable at small bud stage (Fig. 1A) but in later stages, up to fruit set, it expands greatly (Fig. 2D). After abscission this enlarged area appears to collapse and the pedicel diameter becomes smaller. Nuclei are observed to disintegrate.

Pedicels of Menominee at the point of abscission show a smooth break and the crescent-shaped protective layer persists (Fig. 3A). Covering the abscission surface is either a thin layer of gums and waxes, or a layer of desiccated cells.

A flat abscission plane remains in Russet Burbank (Fig. 3B). Many cells and cell fragments are left after abscission, which give the broken surface of the pedicel a ragged appearance. The small quantities of gums and waxes detectable are deposited several cell diameters from the abscissed surface. The surface cells are desiccated.

Examination of the abscission zone showed many important differences from earlier work by Young (4). He stated that the abscission zone swelling was due to division of cells in the cortex, whereas in this study cell divisions were found only at the small bud stage, and subsequent swelling was due to cell expansion. Young stated that the plane of the protective layer curved downward more strongly as the layer matured. In both Russet Burbank and Menominee, the shape of the plane was observed to be determined early and very little change, other than a general size increase, took place as the layer matured.

The greatest difference between this study and Young's was found in the appearance of the vascular system within the protective layer. He stated that the vascular system is bent inward beween the growing areas

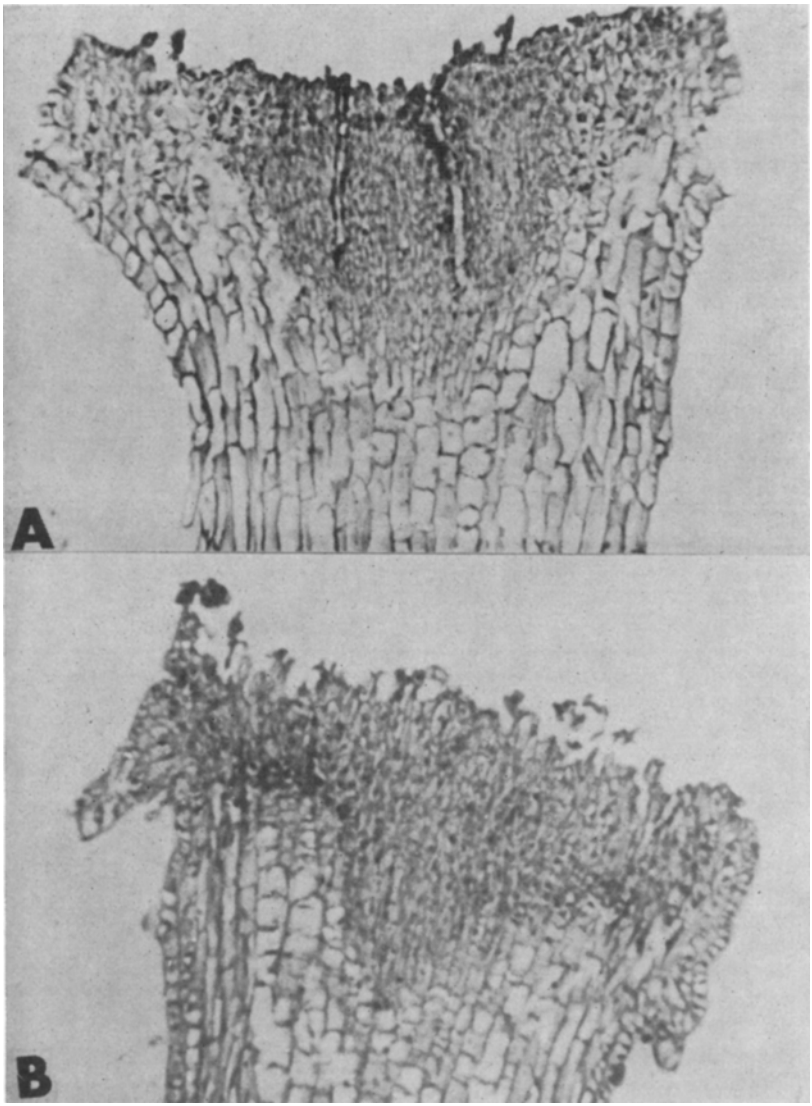

FIG. 3.—A. Menominee, pedicel after abscission of reproductive organ. B. Russet Burbank, pedicel after abscission.

in the pith and cortex. In both potato varieties examined, the vascular system was observed to have a pronounced outward bend. This phenomenon was observed to take place at small bud stage and is believed to have been caused by elongation and expansion of cells between the vascular tissues. Before the protective layer started to develop between the vascular tissues expanded cells were observed. At that time the vascular system had

already been bent outward. Later the protective layer developed in that area.

When the Russet Burbank, which abscisses readily, was compared to the slow-to-absciss variety, Menominee, certain striking differences were noted. In Russet Burbank the pedicels at all stages were small. The protective layer was well developed by small bud stage, but expanded little thereafter. Premature abscission was most often noted at this stage. The abscission zone swelling was already partially developed at small bud stage and was fully expanded by large bud stage. After abscission the end of the pedicel had a ragged appearance.

In Menominee the pedicels were large and robust. The protective layer was not fully developed until flower stage. The abscission zone swelling started to develop at small bud stage and expanded greatly until fruit set. After abscission the end of the pedicel was smooth.

Abscission is known to take place in three ways (1), mechanical breakage, dissolving of the middle lamella, or complete dissolution of cells in the separation layer. Differences in the appearances of abscissed pedicels of Menominee and Russet Burbank may be explained by assuming a difference in the type of abscission. The smooth, cleanly abscissed pedicels of Menominee, indicate a complete dissolution of cells on the separation layer during abscission down to the protective layer. The thin layer of deposits detected on the abscissed surface might be collapsed cell walls. The ragged appearance of Russet Burbank abscissed pedicels might indicate only middle-lamella breakdown in the separation layer. This breakdown would occur in a band of several cell diameters, creating an area of individually separated cells. After abscission some of these cells may be left on the surface and so cause the ragged appearance.

These observations are supported in part by Fig. 1D. Small clumps of loose cells are seen in the separation layer. Many more cells might become loose as abscission progresses.

The abscission zone description points out the fact that Russet Burbank abscission zones developed earlier than those in Menominee. Very early in the development of the bud, the abscission zone reached the point where abscission could take place. This accelerated development may be the indirect cause of premature abscission, for small buds may be more sensitive to small environmental fluctuations. If the abscission zone was developed enough to absciss, any small internal change in plant chemistry might initiate abscission.

The abscission zone study contained several weaknesses. The Russet Burbank pedicels were collected from plants in the warm (75 F) greenhouse, while Menominee pedicels were collected in the cool (70 F) greenhouse. Since Russet Burbank normally abscissed in the bud stage, stages after large bud must have been stimulated not to absciss. Various stages of development were collected from plants grafted to different understocks. There were differences between understocks in numbers of flowers produced; therefore there may be differences in the appearance of abscission zones from different understocks. These shortcomings can, and should be, investigated with further research and corrected if possible.

SUMMARY

Photomicrographs were made of longitudinal sections of flower pedi-

cels. Two varieties, Menominee and Russet Burbank were studied at six stages of development ranging from small bud stage through actual abscission of the reproductive organ.

Generally speaking, a protective layer is formed in both varieties but develops much earlier in Russet Burbank, being completed in small bud stage, while in Menominee it is completed by large bud stage. Actual abscission results from the formation of a separation layer formed from a few to several cells distant from the protective layer. The separation layer results from cell collapse and disintegration; first between the epidermis and the vascular system and finally over the pedicel's entire cross section.

Abscission zones are more pronounced externally in Menominee than in Russet Burbank. A flat surface remains when abscission occurs in Russet Burbank; whereas, in Menominee, a concave or dish-shaped terminus results.

Resumen

Se tomaron fotomicrografías de secciones longitudinales de pedículos de la flor. Se han estudiado dos variedades, Menominee y Russet Burbank, en seis distintas etapas del desarrollo, desde la fase de diminuto brote hasta la de efectiva abscisión del órgano reproductivo.

En sentido general, en ambos variedades hay formación de un estrato protectivo, pero éste desarrolla más temprano en la Russet Burbank, ya que aquí queda cabalmente constituído ya en la fase de brote, mientras que en la Menominee queda finiquitado recién en la fase de brote ya en desarrollo. La abscición efectiva resulta de la formación de un estrato separador formado ya de unas pocas ya de muchas células que distan del estrato protector. Este estrato separador resulta del colapso de células y de su desintegración: primeramente entre el epidermis y el sistema vascular y finalmente sobre toda la sección transversal del pedículo.

Las zonas de abscición son exteriormente más pronunciadas en la Menominee que en la Russet Burbank. Queda, en la Russet Burbank, una superficie llana al ocurrir la abscisoón, mientras que en la Menominee resulta en un término cóncavo o en ahuecamiento del tipo de un plato.

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Literature Cited

1. Eames, Arthur J. and Laurence H. McDaniel. 1947. An Introduction to Plant Anatomy, pp. 266 ff. McGraw-Hill Book Co., New York and London.
2. Johansen, D. A. 1940. Plant Microtechnique. McGraw-Hill Book Co., New York and London.
3. Wenheimer, W. H. and G. W. Woodbury. 1966. Effects of grafting and *Solanum* understocks on flower formation and abscission of flowers and fruits in the Russet Burbank potato. Amer. Potato J. 43: 453-457.
4. Young, W. J. 1922. Some phases of breeding work and seed production of Irish potatoes. S. C. Agr. Expt. Sta. Bull. 210.