with those of Scott et al. (8) obtained in South Carolina, although he incorrectly identified the storage carbohydrate as sucrose. Carbohydrates in storage roots were reduced during harvest and were depleted even more severely during the initial fern production period. Storage carbohydrates were replenished after the fern had matured and had begun to produce sufficient carbohydrate for translocation and assimilation. The effect of extending harvest was to increase the severity of carbohydrate depletion, and to decrease the number of days available through the rest of the season for the production of storage carbohydrates for the succeeding year's growth.

In the second experiment, there was a 6 week period (late July to early September) during which there were no significant differences in percent storage carbohydrate, yet plants harvested for 6 weeks had significantly less total root dry matter than plants harvested for 0 or 3 weeks. It appeared that storage root formation was inhibited by the longer harvest period without the percent storage carbohydrate being significantly affected. Our results indicated that harvest should not begin until 2 complete years following transplanting have passed, and should not exceed 7-9 weeks after the planting is well established.

Asparagus storage carbohydrates are fructo-oligosaccharides, contrary to the report by Scott et al. (8). That fructo-oligosaccharides have existed in asparagus roots has been known since 1909; however, due to problems with methodology, estimates of composition and size have remained tentative. Gas chromatography and gel exclusion chromatography in this study clearly indicated that parent oligosaccharides consisted of $\sim$ 10% glucose, and $\sim$ 90% fructose, with molecular weights not exceeding 4,000. Shiomi et al. (9) performed structural analyses of fructo-trisacchardies through pentasaccharides from asparagus roots; however, structural analyses of the larger oligosaccharides have yet to be attempted.

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An Anatomical and Morphological Study of Abscission in Highbush Blueberry Fruit[1]

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Additional index words. Vaccinium corymbosum, fruit ripening, harvesting

Abstract. **Berry/pedicel abscission zone formation in cultivated highbush blueberry (*Vaccinium corymbosum* L.) during fruit ripening appeared at the distal portion of the transition zone (disc) separating the berry and the pedicel. The abscission zone was first evident as a compressed zone of cells at the periphery of the berry/pedicel junction in the immature green stage of berry development. Cell separation initially appeared during the green-pink berry stage concomitant with berry coloration. Separation was characterized primarily by cell wall rupture. No separation layer was formed through either the berry epidermis or the vascular bundles. The number of berries without attached pedicels separating from the cluster under applied force was closely related to the stage of ripening of the fruit. Stresses imparted during ripening by rupturing internal tissues are evident in definite morphological changes appearing on the surface of the fruit.**

Though research is being conducted on the chemical promotion of blueberry fruit abscission (5), no reports on the nature of fruit separation layer ontogeny during the development and maturation of this fruit have appeared, and only a few on the abscission of other crops have appeared (2, 9, 10). This investigation was undertaken to elucidate the anatomical and morphological changes associated with abscission zone ontogeny in developing highbush blueberry fruit.

Materials and Methods

Morphological study. The point of fruit detachment was determined on mature plants of: 'Blueray', 'Bluecrop', 'Herbert', 'Darrow', 'Coville', and 'Lateblue'. Twenty fruit in each of 5 color stages (described below under *Anatomical study*) were selected and detached by manually applying an even pull-force to the berry in a direction approximately parallel to

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the long axis of the pedicel. The amount of pull necessary to remove the berry was not measured, since we sought to determine only the point of detachment.

The morphology of the abscission zone was studied on 'Coville' berries only. Fruit were examined under a dissecting scope. Photographs of pertinent morphological structures were taken with a Wild Heerbrug M400 Makroskop.

Anatomical study. Samples of fruit for anatomical study were harvested at weekly intervals from full bloom to green-pink and daily thereafter, throughout the 1977 season from healthy, mature bushes of 'Earliblue', 'Collins' and 'Coville' cultivars. Berries with pedicels attached were cut from the peduncle and visually separated into color stages: immature green (IG), mature green (MG), green-pink (GP), blue-pink (BP), blue (Bl) and ripe (R). The immature green stage included the largest berries with a dark green color over 100% of their surface. Mature green berries were a light greenish-white color with the calyx just beginning to turn pink. Berries in the green-pink stage were 75% green and 25% pink. Blue-pink berries were 75% blue and 25% pink. Blue berries were blue over 90% of their surface and approximately 10% pink around the future scar. Ripe berries were blue over 100% of their surface. Extraneous material such as adhering corollas or pedicels was trimmed from the berries prior to fixing.

Samples were fixed in Randolph's Modified Navashin solution, dehydrated through an ethanol/t-butanol series and embedded in Paraplast-Plus. Tissue was sectioned at 15 μm and stained with Heidenhain's Iron Alum Hematoxylin. Photomicrographs were taken with an AO Microstar Microscope fitted with a #545 Polaroid Attachment.

The terms "abscission zone" and "separation layer" are used in accordance with the definition of Esau (6): "Abscission zone" refers to the tissue region through which the "separation layer" forms. The term "separation layer(s)" refers to the one or two cell layers through which an actual break occurs. The term "disc" as used in this paper refers to the swollen disc-shaped area on the distal portion of the pedicel immediately proximal to the berry. This area includes a tissue transition zone composed of both pedicel-like and berry-like tissue.

To determine the relative enlargement of cells in the berry/pedicel abscission zone and contiguous zones throughout two stages (GP, and Bl) 5 cells in each of 4 locations on each of 3 longitudinal cross-sections of each color stage of 'Earliblue' were measured with an ocular micrometer. The area of each cell was calculated by using the formula for the area of a circle ($A = \pi r^2$) or for the area of an ellipse ($A = 0.7854$ (ab)) where "a" is the length of the long axis and "b" is the length of the short axis. All cells were located in the central cortical regions of each location. The 4 locations (Fig. 3A) were:

1. pedicel, proximal to and contiguous with the disc
2. medial portion of the disc
3. disc, proximal to and contiguous with the berry
4. berry, distal to and contiguous with the disc.

Results

Morphological study

Fruit detachment. Fruit of 6 cultivars behaved similarly in regard to point of detachment. Therefore, data for 'Bluecrop' only are presented (Fig. 1). Berries in the IG stage of maturation nearly always separated from the peduncle with the pedicel intact when placed under an applied force. As ripening continued an increasingly greater percentage of berries separated at the berry/pedicel junction. The percentage of berries separating at the pedicel reached the midway point at approximately the "GP" stage of ripeness. That is, about 50% or more of the berries that had some red coloring separated from the pedicel. Berries in the "Bl" stage of development nearly always separated from the pedicel. This would seem to suggest that a reasonably weak abscission zone existed at the pedicel/peduncle junction during the early stages of berry development. During fruit development a second abscission zone developed at the berry/pedicel junction. It is at this second zone that separation of ripe fruit from the plant occurs at harvest. Further study on the ontogeny of the pedicel/peduncle abscission zone is in progress.

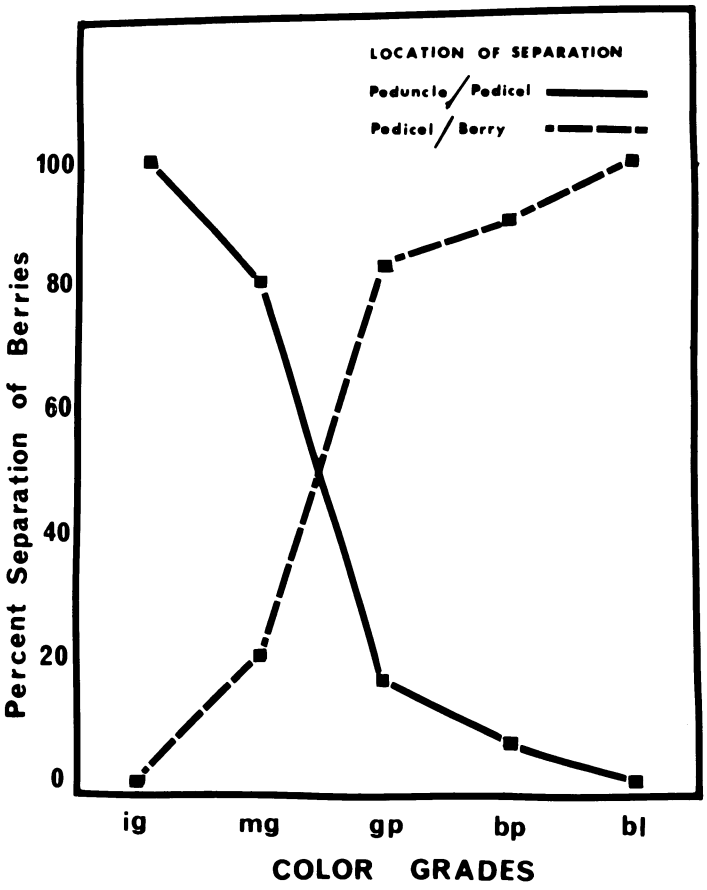

Fig. 1. Location of separation point of 'Bluecrop' blueberry fruit in 5 stages of maturity and ripeness.

Abscission zone of the berry/pedicel junction. The point of attachment of the pedicel to the berry is located in a cavity about 5 mm in diameter at its surface rim and narrowing to about 2 mm in diameter at its lowest point. The cavity is about 2 mm in depth. Cavity dimensions remained unchanged throughout fruit ripening. A discription of changes in this area (Fig. 2a-f) is as follows:

1. IG STAGE. In this early stage of fruit development, the cavity walls are nearly completely covered with bloom showing what appears to be radial stress marks (sm) as indicated by lines of broken bloom radiating from the center of the cavity. This may be attributed to the expansion of the fruit tissue around the attachment point and the differential developmental processes between the fruit and the pedicel. The disc (D) also shows radial stress lines indicating that it too has begun to increase in size, perhaps at a rate differing from surrounding tissue. A ring of berry epidermis possessing no bloom is apparent peripheral to surrounding the disc.

2. MG STAGE. (Fig. 2b). Morphology of the abscission area is essentially the same as in the IG stage, except that the disc has enlarged and extended over the surface of the berry. Radial stress marks are more apparent than those in the IG stage.

3. GP STAGE. (Fig. 2c). The disc has continued to enlarge and a greater number of radial stress marks are apparent on

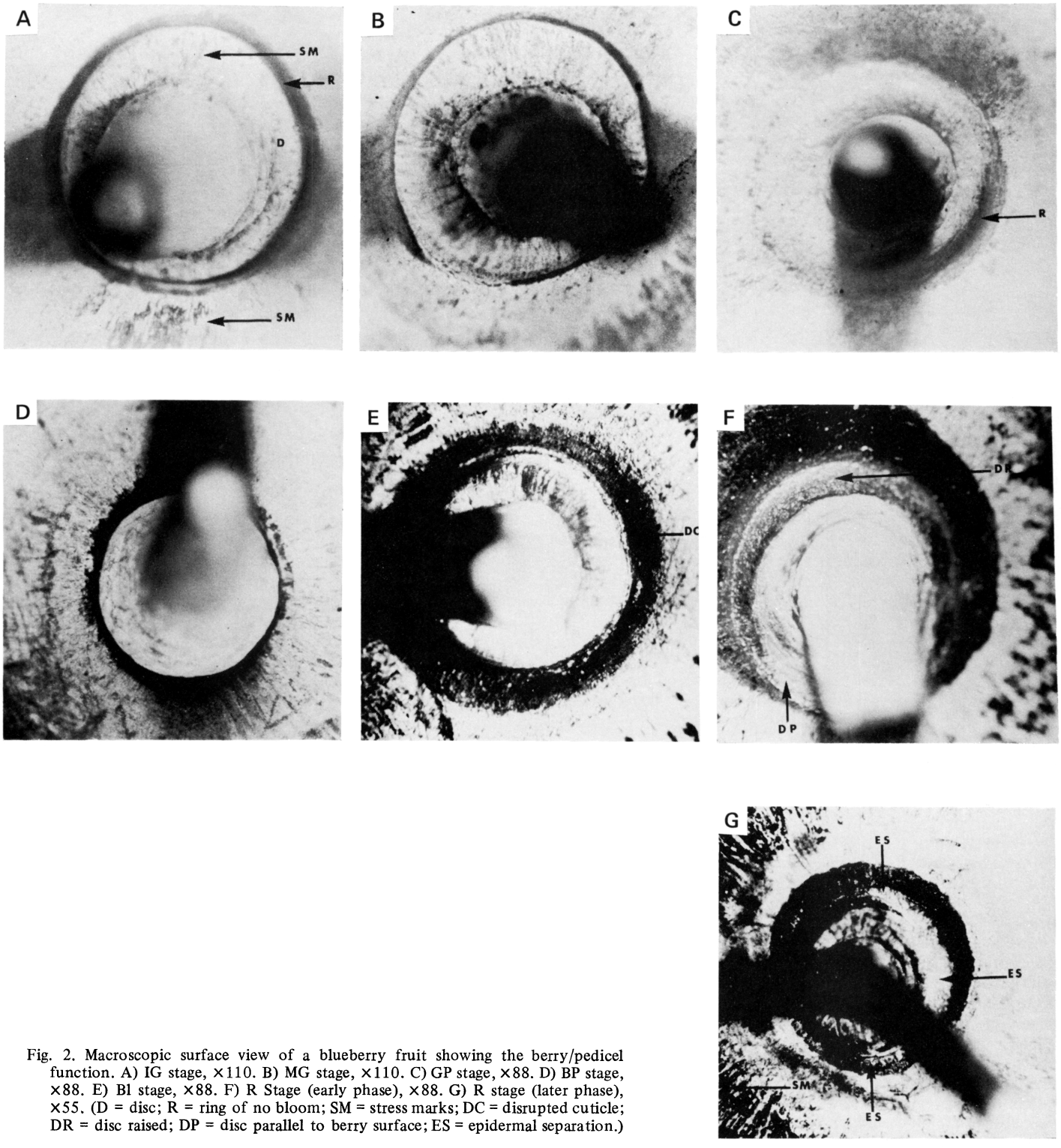

Fig. 2. Macroscopic surface view of a blueberry fruit showing the berry/pedicel function. A) IG stage, ×110. B) MG stage, ×110. C) GP stage, ×88. D) BP stage, ×88. E) Bl stage, ×88. F) R Stage (early phase), ×88. G) R stage (later phase), ×55. (D = disc; R = ring of no bloom; SM = stress marks; DC = disrupted cuticle; DR = disc raised; DP = disc parallel to berry surface; ES = epidermal separation.)

both the disc and the berry epidermis. The outer edge of the disc develops some red coloration during this stage. However, the portion of the disc proximal to the pedicel remains green although red coloration does appear on the exposed side of the pedicel. A distinct green zone lacking bloom is still apparent between the disc and the berry. Appearance of the disc would indicate that pigment development is apparently initiated here at about the same time as in the berry. Also, the concentricity of the lower portion of the cavity is noticeably disrupted in some specimens at this stage of development. Instead of being circular at the base, the cavity may be more elliptical. This disfiguration may be due to a weakening of the tissue connected to the disc.

4. BP STAGE. (Fig. 2d). Though the ring of berry epidermis lacking bloom peripheral to the disc is still quite noticeable, it has now assumed the pink color of the berry tissue immediately

Table 1. Mean cell areas in 4 locations in the pedicel/berry junction and % increase of cell areas during fruit ripening of blueberries, 'Earliblue', 1977.

Stage of ripeness	Area 1[z] Mean (μm^2)	Area 1[z] Increase[y] (%)	Area 2 Mean (μm^2)	Area 2 Increase (%)	Area 3 Mean (μm^2)	Area 3 Increase (%)	Area 4 Mean (μm^2)	Area 4 Increase (%)
Green pink (GP)	1145	0	1042	0	2081	0	3798	0
Blue (Bl)	2193	92	2207	112	5194	150	9412	150

[z]Area 1 – Pedicel proximal to disc, Area 2 – Medial cortical disc section, Area 3 – Disc/berry junction, Area 4 – Berry distal to disc.

[y]Percent of area increase over the green-pink stage.

surrounding it. The disc has become noticeably more red, following pigment development in the berry.

5. BL STAGE. (Fig. 2e). The disc has become primarily deep red and the ring lacking bloom has become noticeably wider and more distinct, being about 0.5 mm wide along the cavity wall and extending approximately 0.25 mm up the disc wall. Although the ring is essentially deep red in color, certain portions possess discreet areas of blue pigmentation.

The boundary of the ring and the disc is marked by a band of disrupted, flaking cuticle (DC) about 0.12 mm in width which is apparently due to the stress imparted on the area. The integrity of the cuticle is apparently disrupted to a greater extent on the side of the disc receiving the greatest tension from the hanging berry. The cuticle on the side receiving compression force appears visually to be unaltered.

6. R STAGE. (Fig. 2f). The berry and pedicel begin their final process of separation by beginning to actually "pull away" from each other during the early phases of this stage. The ring has increased in both width and in blue coloration. The disc itself is noticeably raised, with walls in some locations nearly perpendicular to the berry surface. These walls remain predominantly red in color, while the remainder of the disc oriented parallel to the berry surface develops blue color and an obvious bloom. The perpendicular disc walls again occur on the portion of the disc receiving the most tension from the hanging berry. This, along with the observation that the ring of disrupted cuticle now completely surrounds the disc, suggests that internal integrity of the berry/pedicel junction has deteriorated almost completely, placing excessive stress on the berry epidermis.

7. LATER PHASES OF THE RIPE STAGE. (Fig. 2g). These are characterized by a nearly complete loss of integrity in the cell layers surrounding the disc. Epidermal separation (ES) occurs in areas under tension along the line of juncture between the disc and the ring which was characterized in earlier stages by a disrupted cuticle. The disc is dark blue and the pedicel often deep red at this phase. In many cases a distinct swelling of the pedicel becomes apparent at the pedicel/disc junction. Also, in this terminal stage the cavity becomes noticeably less distinct, again perhaps indicating an internal loss of integrity. The epidermis contributes little to fruit attachment.

Anatomical study

Data are presented for 'Earliblue' only, since the fruit of all cultivars underwent similar developmental patterns. Differential cell enlargement was apparent among the 4 areas of the pedicel/berry junction studied (Table 1). Cellular measurements varied greatly, but, in general, indicated about a 100% increase in cell size during ripening in both Area 1 and 2. However, cells in Area 3 increased 150%. This corresponds well to the increase in cell area of berry cells near the disc (Area 4) although cells in Areas 3 and 4 were initially of different areas. Hence, cells in certain areas of the disc undergo size increases comparable to those of the berry during ripening.

Vascular system (Fig. 3). The vascular system of the pedicel undergoes divergence in Area 3 at about the point of invagination marking the disc/berry junction (Fig. 3a). At this point, or slightly proximal to it, the degree of vascular sclerification noticeably decreases. Protophloem fibers are absent and the number of brachysclerids in the berry is diminished. In addition, the pedicel pith becomes discontinuous. The combination of all these features, therefore, may make the transition zone inherently structurally weak.

Cortical region. Outer cortical regions of the disc remained similar to those of the pedicel until Area 2, distal to which was fairly rapid reduction in subepidermal layers from several in the pedicel to 1 or 2 in the berry (Fig. 3b, c, d). The interior layers of the disc are composed of parenchymatous tissue similar to that of the berry. However, a difference in cellular characteristics within the disc is apparent according to variations in staining properties of the cells. This difference is particularly prominant in later stages of ripening (Fig. 3b, c, d). Area 1 of the disc is composed of smaller, more deeply staining cells similar to those of the pedicel cortex, while cells in Areas 2 and 3 stain progressively more like those of the berry (lighter).

As mentioned above, cortical cells of the disc undergo differential enlargement as ripening proceeds. This may result in a substantially weakened cell condition that would facilitate cell rupture under the stress of berry enlargement. Cortical cells in Areas 2 and 3 of the disc demonstrate the stress imparted by both disc and berry enlargement, being oriented in a position approximately perpendicular to the short axis of the berry. Compression and tension both increase until, by the R stage, some cortical cells in both areas 3 and 4 have ruptured (Fig. 3c) with partial alignment of fragmentary walls along the fracture.

Abscission zone. The abscission zone is first evident as a constricted and somewhat compressed zone of cells at the periphery of the pedicel/berry constriction in the IG stage of berry maturity (Fig. 3a). However, the beginning of berry separation was not anatomically evident until the fruit had attained the GP stage of ripening, and was complete by the R stage (Fig. 3b, c, d). The zone of initial separation was centered within the area of vascular divergence. Further development of the abscission area appeared in longitudinal section as a crescent extenting across the distal portion (berry side) of the disc. It did not, however, develop across the vascular tissue or the epidermal tissue of the disc. The area of this crescent was characterized essentially by cell wall rupture and to some extent by cell separation. No noticeable cell division was involved. This may be attributed to the disc actually pulling away from the berry, as illustrated in Fig. 2f, since the distal boundary (invagination) of the disc is shown in Fig. 3c and d to have become rather indistinct.

Although it would appear in early stages of ripening that a true separation layer forms, this layer does not develop

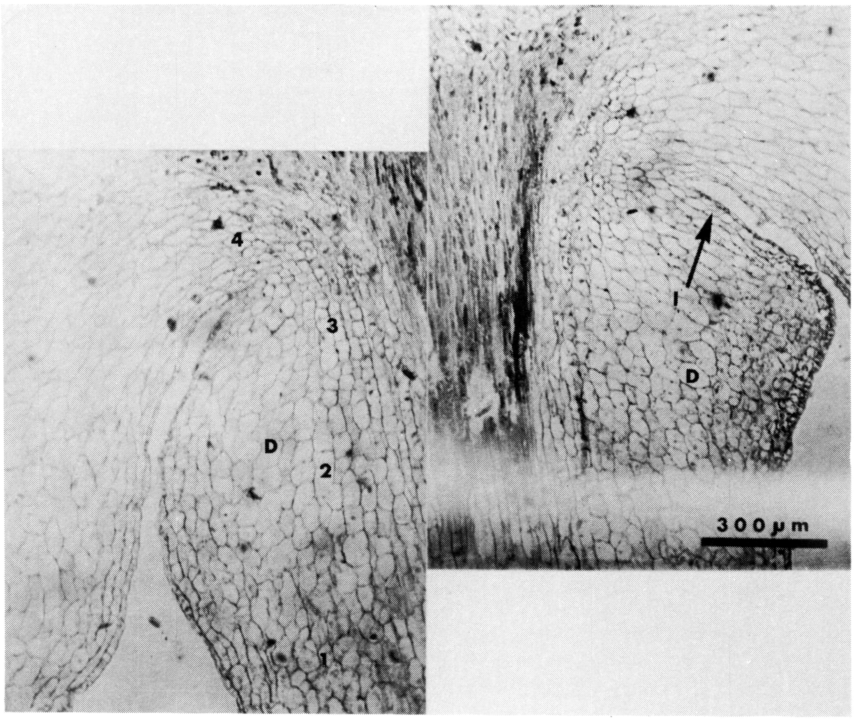

Fig. 3A. IG Stage. Microscopic longitudinal section of a blueberry fruit showing the berry/pedicel junction and development of the disc and the abscission zone. (A = wall fragments; B = initial tissue breakdown; D = disc; I = invagination; SE = subepidermal layers; BA = brachysclerids; 1, 2, 3, 4, – Disc areas.)

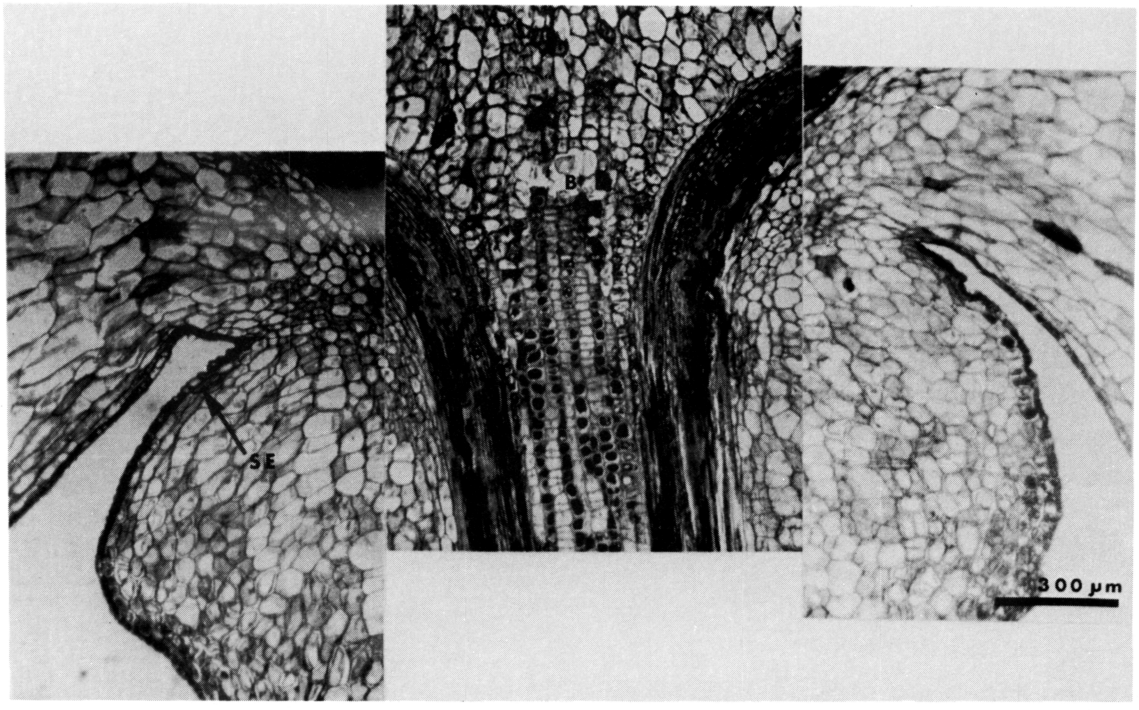

Fig. 3B. GP Stage.

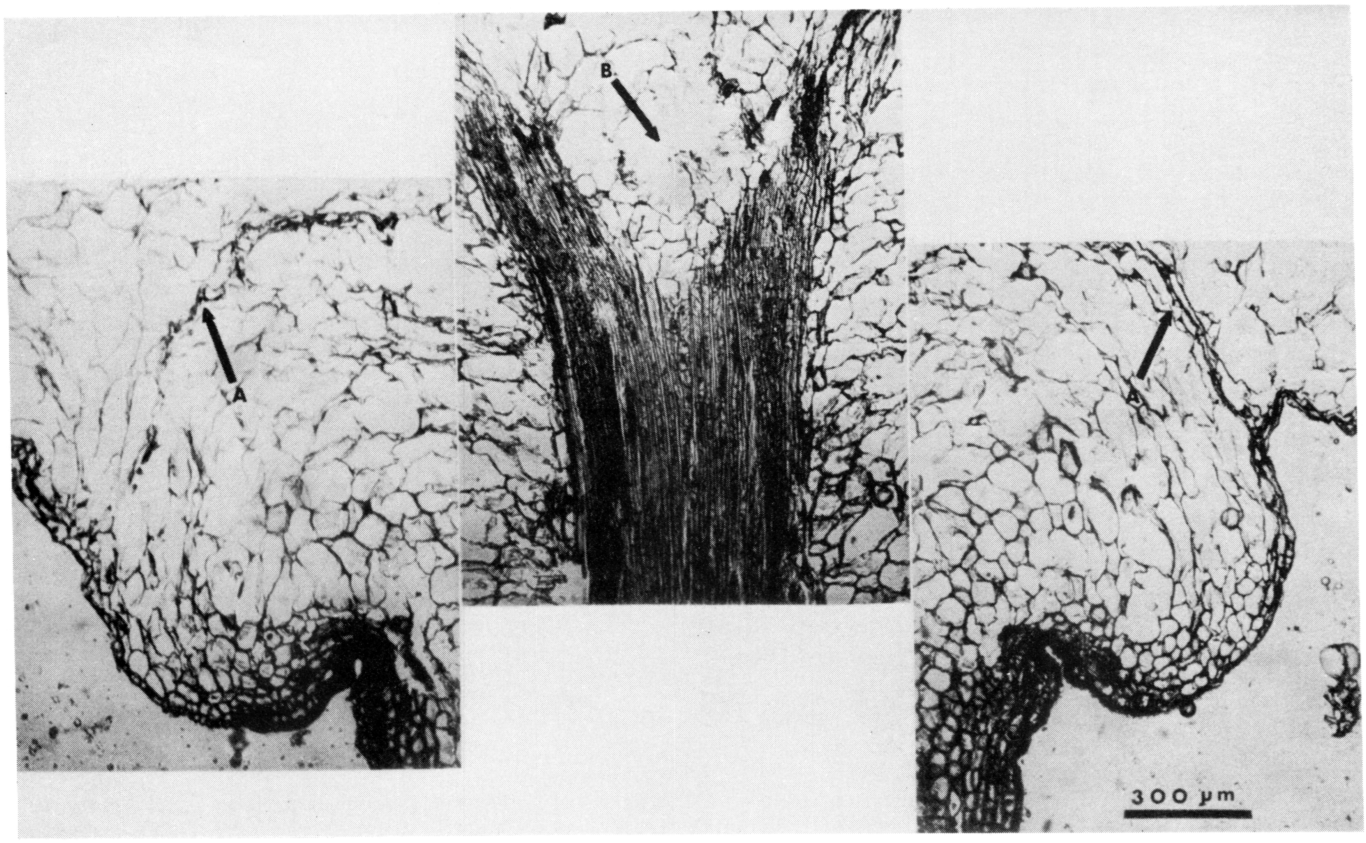

Fig. 3C. R Stage (early phase).

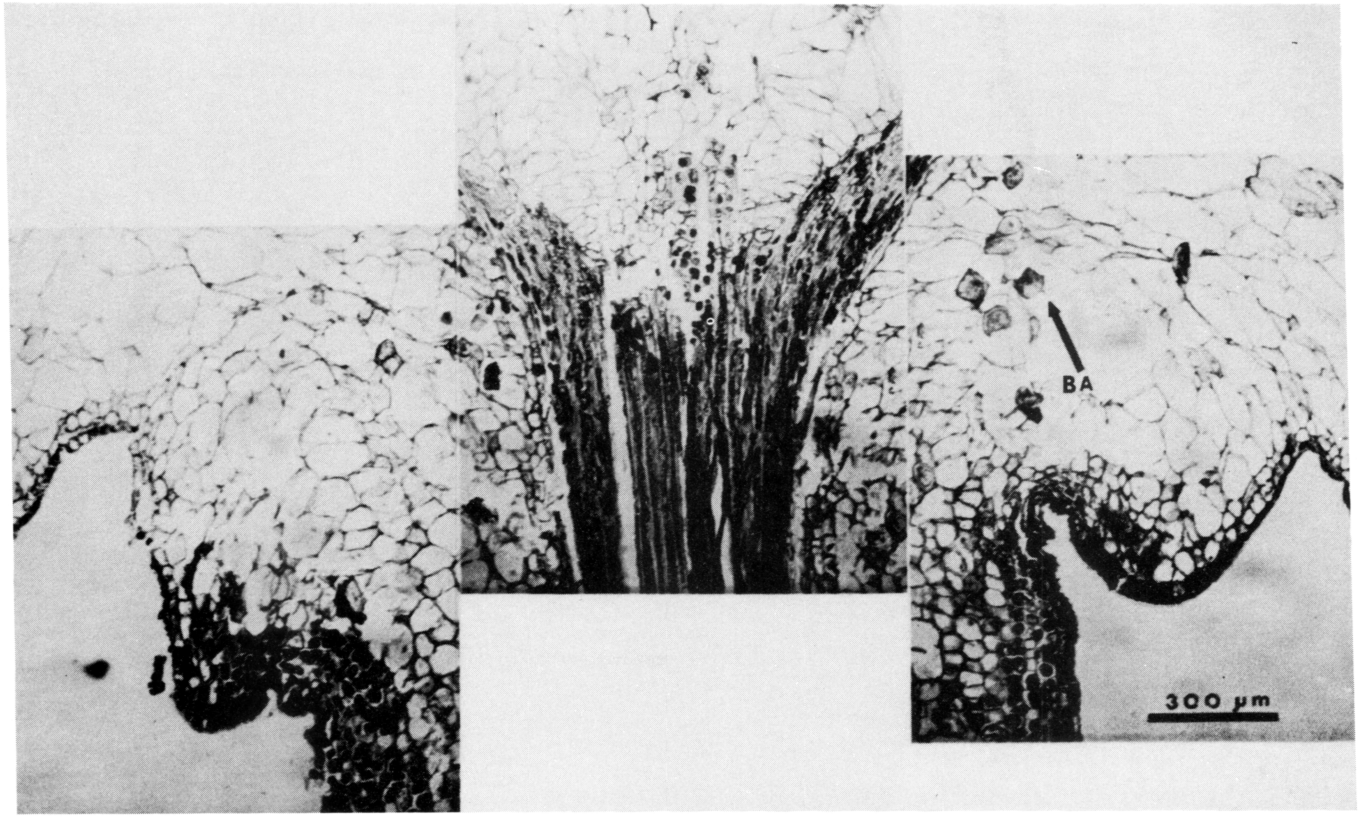

Fig. 3D. R stage (later phase).

further. Therefore, preparation for final separation is due to cellular disintegration in a zone rather than the formation of a discreet layer.

Discussion

The site of separation-zone formation in different fruits varies considerably. Pome fruit abcise at the pedicel base (7, 8). Plum fruit may be shed with or without pedicels (4). Two abscission zones are known in sweet cherry (9). Cherry fruit may abscise between pedicel and peduncle or between peduncle and spur, depending upon time of year. Fruit separation at maturity occurs at the fruit base in mango and avocado (2) and in orange (10).

A morphological and anatomical study of the zone of abscission in the highbush blueberry indicates that the zone has tissue that is both inherently dissimilar to contiguous tissue of the pedicel and the berry and structurally weak. Anatomically, the disc at the point of attachment of the pedicel and the berry was composed of transitory tissue, some of which possessed certain properties of both pedicel and berry as illustrated by differential cell enlargement, sub-epidermal layer differences, and sclerification differences. Separation by cell wall rupture occurs near the distal region of this disc. The initial disruption of tissue integrity in this region was evident at approximately the Green-Pink stage of berry ripeness. Further loss of integrity and eventual separation rapidly developed through subsequent stages of ripeness. The onset of berry coloration (green-pink stage) was also the approximate stage of ripeness at which most berries separated with applied force at the berry/pedicel junction rather than the pedicel/peduncle junction. Therefore, the berry could be loosened from the pedicel when it began to develop red color. In combination with the loss of cellular integrity in the abscission area, added stress is also placed on the structurally weak area by the differential expansion of cells in the transition zone and by the increased point stress due to the increase in fruit weight. Since the structural integrity of the vascular system and the epidermis is apparently not altered, final fruit separation is brought about by mechanical rupture of these tissues. Histological changes in separation zone formation in the blueberry are similar to those in other fruit (9) and other organs (1, 3).

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Seedless Fruit in 'Fuerte' and 'Ettinger' Avocado[1]

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Additional index words. ovule degeneration, endocarp, *Persea americana*

Abstract. **Seedless fruitlets of 'Fuerte' and 'Ettinger' avocado (*Persea americana* Mill.) (5 to 20 mm length) exhibited a typical degeneration pattern of the ovule which began at the chalaza and spread toward the micropylar region but stopped when about half of the integument was still intact. Embryo or endosperm or both were found in many seedless fruitlets. Degeneration was found to start at different stages of fruitlet development, from a proembryo to an embryo starting to develop cotyledons. Typical seedless fruit in 'Fuerte' and 'Ettinger' avocado appears to be the outcome of seed degeneration (stenospermocarpy) and not parthenocarpy.**

Seedless fruit (cukes) occur frequently on 'Fuerte' (Fig. 1) and 'Ettinger' trees (3, 7). The number of seedless fruit varies yearly, the amount usually being larger when fruit set of normal seeded fruit is very poor or following girdling which increases the amount of both seeded and seedless fruit (5, 8). Anatomical examination showed that the small body at the distal end of the seed cavity is a partially degenerated seed coat (3). Seedless fruit may be the result of either automatic parthenocarpy or stenospermocarpy (fruit development after embryo abortion). Seedless fruits were examined to determine the type and mode of carpel development in seedless avocado.

Materials and Methods

It is possible to recognize seedless fruitlets on the tree, when they are ⩾20 mm in length by their elongated shape and small size compared with seeded ones. Earlier identification of seedless fruitlets at 5 mm in length could be made by cutting the distal part of the fruitlet, revealing the typical cavity of the seedless fruit. The ovule is degenerated in most fruitlets containing cavity and it is difficult to identify any structure within the ovule. Seedless fruitlets 5 to 20 mm long from 'Fuerte' and 'Ettinger' trees were sampled during April and May from 3 different orchards (Kibbutz Rosh Haniqra, Kvuzat Schiller and the Agricultural Research Organization, Bet Dagan). The

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