

Structure and Development of Surface Deformations on Avocado Fruits

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Abstract. Avocado (*Persea americana* Mill., cv. Simmonds) flowers and fruitlets were histologically examined to characterize the development of disfiguring bumps and ridges, as well as to investigate possible causes of the disorder. The outer cell layers of the ovary are damaged by a small, surface-feeding insect during and soon after anthesis. Bumps and ridges form as a result of cell proliferation in the pericarp directly beneath the wounds. Circumstantial evidence suggests that two species of flower thrips (*Frankliniella*) are the possible causal agents.

The West Indian race of avocado includes several commercial cultivars produced in southern Florida. A major problem associated with production of these cultivars is excessive gradeouts due to deformed fruit. Numerous, large bumps and ridges reach several millimeters to a centimeter above the surface of mature fruit (Fig. 1A) and distinguish deformed from normal fruit (Fig. 1B). Deformations are first noticeable in young, developing fruitlets (Fig. 1C). Deformations appear to grow in proportion to the overall growth of the fruit. The apex of each bump generally bears a small surface scar <0.5 mm in diameter. The peaks of ridges are also characterized by surface scarring of the exocarp.

Although the problem occurs in other cultivars of West Indian origin, as well as those of the Guatemalan race and its hybrids, it is most apparent in the popular West Indian cultivar, Simmonds. At times, >50% of the harvest may be culled at the packinghouse due to badly disfigured fruit. The severity of the problem varies from year to year. In some years, the entire harvest of a grower has been rejected (N. Sutton, personal

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communication); however, the development of disfigured avocado fruit in southern Florida has not been described.

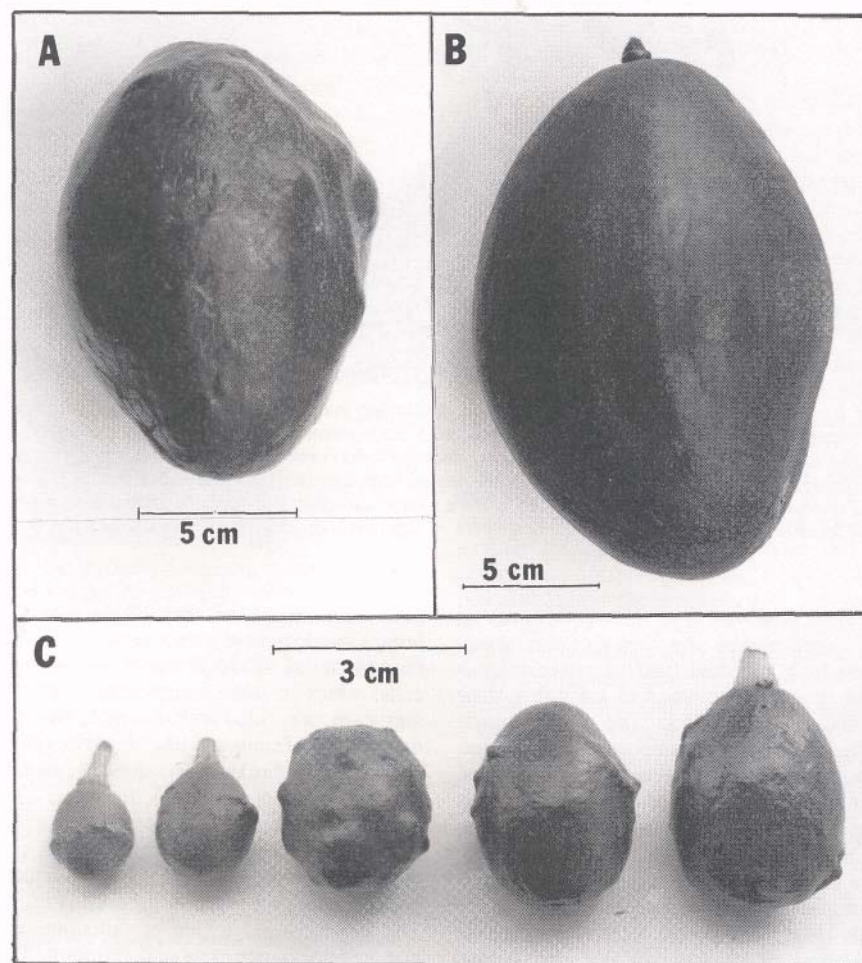


Fig. 1. Surface deformations on avocado fruits. (A) Deformed, mature fruit. (B) Unaffected, mature fruit. (C) Deformed, developing fruitlets.

We detected early development of the surface bumps in fruitlets with a x 10 magnifying lens within 2 weeks after anthesis. This observation suggested that initiation of the deformation occurs at or near flowering time. This study was, therefore, conducted to characterize the timing and early histological development of the bumps.

Flower and fruitlet samples were collected from an orchard in Dade County, Fla., containing 'Simmonds' avocado trees that were showing early symptoms of the problem in developing fruitlets. 'Simmonds', a typical "A" flowering-type cultivar, undergoes dianthesis, i.e., individual flowers open during the morning hours of the first day as functional females and open as functionally perfect flowers during the afternoon hours of the following day (Davenport, 1986, 1989). Flowers were collected during the first and second floral openings, as well as during the closed period (morning of the 2nd day) between openings. They were also sampled \approx 1, 3, 5, and 7 days after anthesis (timed from the second floral opening). These times were estimated based on the degree of petal senescence. Bumps and ridges on developing fruitlets ranging in diameters from

≈0.5 to 2.5 cm were also sampled. It was difficult to estimate ages at these later stages because age and size of fruitlets were not strictly correlated. Whole flowers, small fruitlets, and malformed sections of larger fruitlets were cut and immediately fixed in FAA for at least 48 hr. The material was dehydrated in a tertiary-butanol series, imbedded in Paraplast (melting point, 56-57°C), serially sectioned at 10 μm, stained either with safranin and fast green or with toluidine blue 0. Hand sections were also stained with aqueous toluidine blue 0 or alcoholic sudan IV (Johansen, 1940).

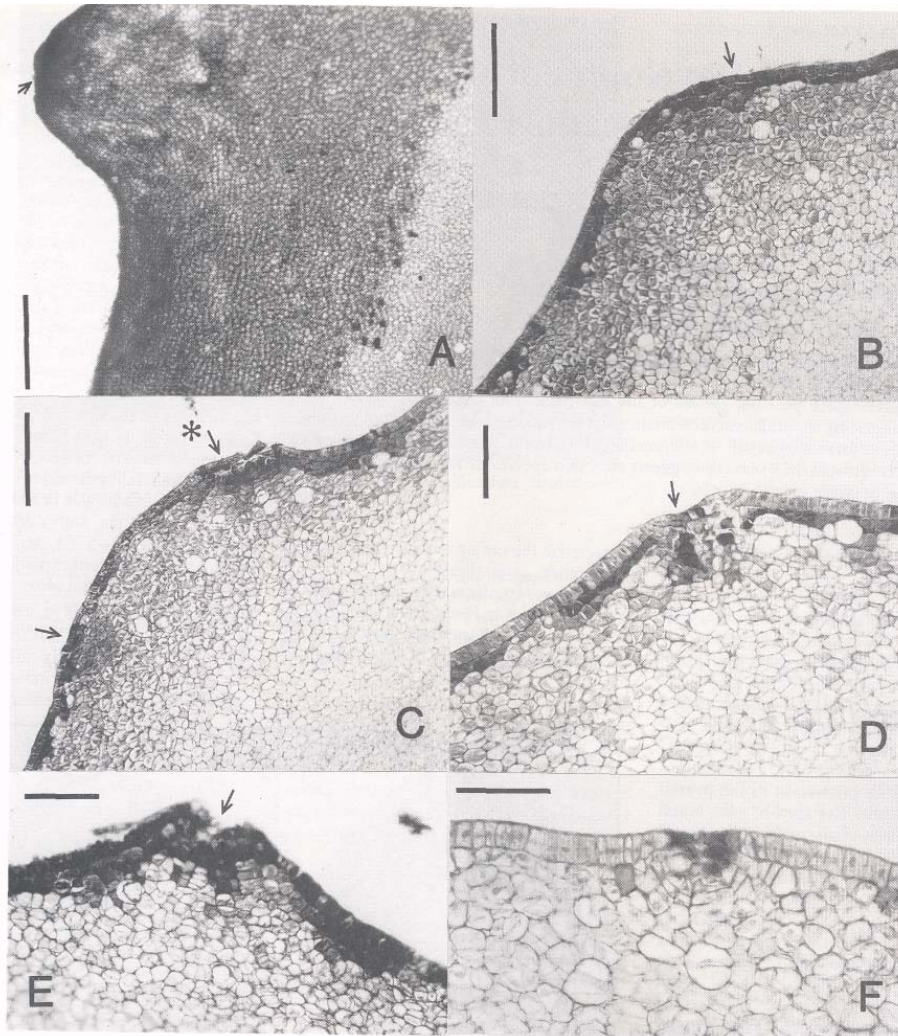


Fig. 2. Thin sections of bumps and ridges on developing avocado fruitlets. (A) Large swelling with surface necrosis (arrow) on a fruitlet ≈3 cm in diameter. (B and C) Swellings on two fruitlets ≈0.5 cm in diameter, with surface lesion (arrows) and some radial cell alignment (asterisk) in the mesocarp cells of the ovary. (D) Swelling with deeper necrotic lesion (arrow) and radially aligned mesocarp cells in 0.5-cm-diameter fruitlet. Dark hypodermal cells are not associated with formation of the wound response. (E) Pronounced bump with epidermal necrosis and disruption (arrow) in fruitlet ≈0.2 cm in diameter, ≈7 days after anthesis. (F) Surface wound and early cell divisions before formation of bump in fruitlet bearing fully dried petals, >0.2 cm in diameter, ≈5 days after anthesis. Scale bars = 0.5 mm (A); 250 μm (B and C); 125 μm (D and E); and 75 μm (F).

Initial observation of thin sections across the raised bumps and ridges of the larger sized fruit indicated that the raised regions were typically composed of a rough surface wound, <1 mm thick. The normal, unaffected exocarp was composed of the epidermis, subepidermal parenchyma cell layers, and an irregular zone of sclerenchyma cells that delimits the inner boundary in the maturing fruit (Cummings and Schroeder, 1942). The raised areas were produced by a proliferation of exocarp and underlying mesocarp cells (Fig. 2A). In the deformed areas, the epidermis of the exocarp appeared normal except

for epidermal cell damage and associated suberization (positive sudan and safranin staining) at the apex of the ridges or bumps in apparent response to an earlier surface wounding. The localized region of dead cells, which in some bumps spread into the mesocarp, was filled with orange-brown pigmented or safranin-staining deposits (probably polyphenolics) and occasionally extended many cell layers deep into the tissue. The cells residing beneath the wound generally exhibited a characteristic cell division pattern of files radiating from the necrotic cells and spreading inward into the fruit (Fig. 2). The subepidermal region of radiating cells had the appearance of wound periderm. This localized proliferation diverged from the normally diffuse cell division patterns of the unaffected avocado pericarp (Valmayor, 1967). The mesocarp beneath large bumps and ridges was raised and followed the contours of the exocarp. Thus, on mature fruits, the bumps and ridges were visible in the mesocarp after the exocarp was peeled off. We examined thin sections of bumps in progressively smaller and younger fruitlets in an effort to determine their origin. In each case, the bumps and ridges displayed the characteristic surface lesion and cell proliferation, regardless of the size of the bump (Fig. 2A-F). In some cases, the epidermal cells were intact (Fig. 2 B-D, arrows), while in others, a physical break in the epidermis had occurred (Fig. 2C, star; Fig. 2E, arrow).

By examining thin sections taken from flowers sampled at various times after anthesis, we found the earliest evidence for a lesion, without the attending bump, on an ovary harvested \approx 5 days after anthesis (Fig. 2F). The cells beneath the lesion did, however, exhibit the initial cell divisions that would presumably develop in the same manner as in older fruitlets. Evidence suggested that a lesion was initially made on the surface of the ovary and extended from the epidermis to no more than three to four cells below — possibly due to the action of a small, shallow-piercing or rasping type of feeding arthropod. The lesion that induced cell division thus occurred earlier than 5 days after anthesis. We observed some surface lesions in younger fruitlets, but we could not determine if these lesions would have been associated later with cell divisions. The wound response differed from wound periderm because of the proliferation of cells far beneath the surface wound and the radiating cell division pattern that developed in subsequent growth of the ovary wall. Typically, surface wounds resulting from physical damage did not elicit such an extensive cell division response in these fruits. No fungal hyphae nor obvious bacterial cells were found in any sections, so we eliminated these as potential causal agents.

In sectioned flowers, mature larvae and vacated egg sacs of an insect were commonly observed in the tissues of pedicels (Fig. 3A), receptacle bases (Fig. 3B), and outer surfaces of the sepals and petals, indicating oviposition activity prior to anthesis. In only a few of many sectioned flowers were there ovipositions in the pistil; these were always in the style or apical region of the ovary (Fig. 3C). In none of these cases did the plant respond by subepidermal cell division, as they did at the apparent feeding sites.

Two species of mirids identified by Leston (1979), *Dagbertus fasciatus* (Reuter) and *D. olivacious* (Reuter), have been suggested to be the causal agent of the disorder (Ruehle, 1958; Wolfenbarger, 1963). More recent research, however, has demonstrated that mirid damage is not correlated with the formation of bumps on the fruit. Mirid damage not only results in a different wound response by the fruit, but fruit deformation

occurs in the absence of mirids through flowering and fruit development (R.M. Baranowski, personal communication).

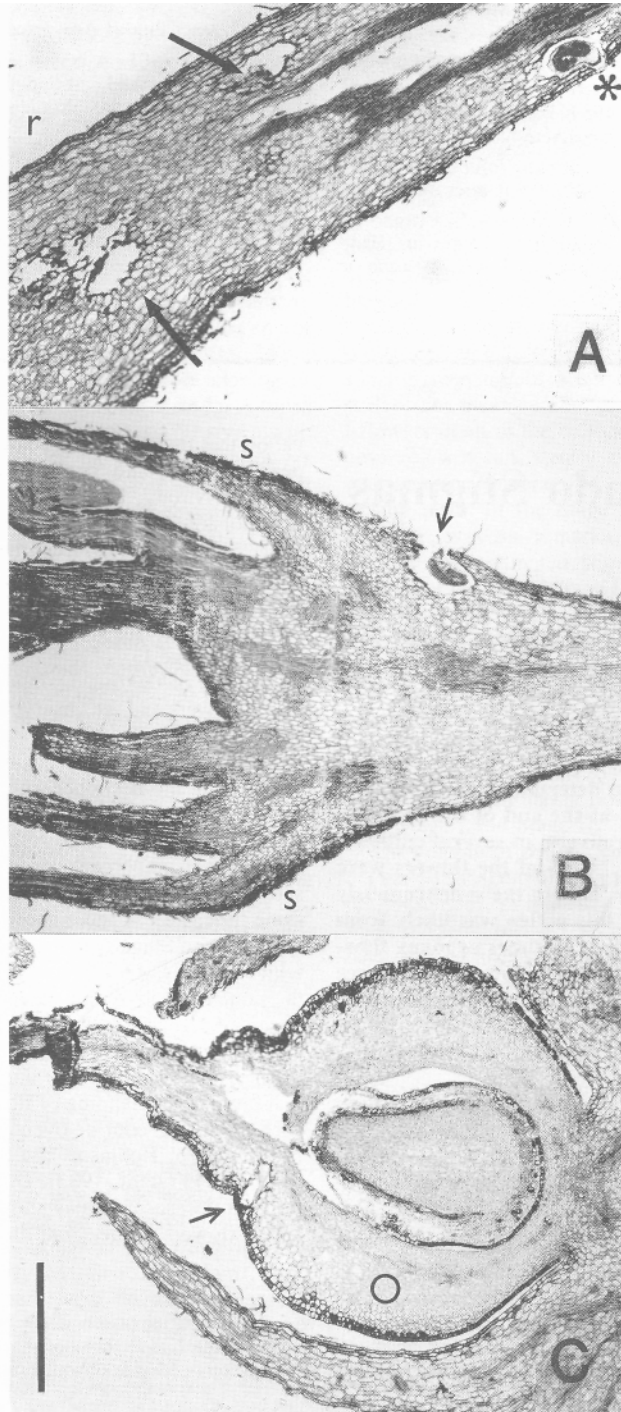


Fig. 3. Oviposition sites of insects in avocado flowers. (A) Pedicel of avocado flower harvested 3 days after anthesis with an egg (asterisk) and cavities vacated by emerged insects (arrows). (B) Receptacle of avocado flower harvested during interval between floral openings with insect egg (arrow) imbedded in cortical tissue. (C) Longitudinal section of avocado flower harvested 3 days after anthesis showing vacated oviposition cavity in base of style (arrow). Scale bar = 500 μ m (A-C). r = receptacle, s = sepal, o = ovary.

Many eggs and developing larvae of the flower thrips, *Frankliniella bispinosa* Morgan

and *F. kelliae* Sakimura, were found in the flowers. Besides the flower thrips, no other small arthropod species were found in the flowers or on the small fruitlets. The former species is known to inhabit avocado flowers in large numbers in southern Florida. The second species of flower thrips has only recently been described (Sakimura, 1981). They feed on and oviposit in tender reproductive growth. Thrips are known to feed by puncturing cells with their short stylet and sucking the exuding sap (Leston, 1979). Our findings suggest that the disfiguring bumps and ridges found on avocado fruit produced in southern Florida are a result of feeding damage by the thrips *F. bispinosa* and *F. kelliae* that are present in the flowers. The cell divisions in the outer pericarp appear to be in response to damage by insects feeding on the outer two to three cell layers of the ovary during and soon after floral anthesis. We suggest, but cannot confirm, that feeding insects may pierce the tissue at a single location, giving rise to bumps, or may graze across the ovary surface, thus causing ridges. Cells presumably disrupted by the insect stylet appear to be killed (Fig. 2D). As the underlying tissue expands, the disturbed area of dead cells may be further disrupted to accommodate the expanding bump, thus enlarging the area of tissue disruption (Fig. 2E). Confirmation of the induction of fruit deformation by flower thrips must await future controlled experiments that introduce or exclude thrips from avocado flowers. Whatever causes, the surface wound also elicits a cell-division response that is analogous to a new meristematic center located directly beneath the wound. This growth response may be due to a specific plant growth-regulating compound injected by an insect or to an injected microorganism that produces such a compound.

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