

Letter to the Editor

Watermelon Stripes. A Case for the Clonal Mosaic Model in Plants

Coat patterns of stripping, banding, and reticulation in animals have been analyzed in detail (see review of [Walter et al., 1998](#)) while in plants only one case of leaf banding has been inspected developmentally ([Korn, 1997](#)) leaving longitudinal stripping essentially unexplored. A common case of stripping is found in the watermelon, *Citrullus lanatus* (Thunb) Matsum. & Nakai, that by even casual inspection appears to involve several interrelated patterns (Figs. 1A and 2A), the genetics of which have been somewhat resolved ([Gusmini and Wehner, 2005](#)). In the cultivar *C. lanatus* Ruby Red these patterns are best observed as, first, an alternating sequence of medium green and light green stripes around the melon (Fig. 1A), next, a dark green reticulum runs the length of the medium green stripe (Figs. 1A and 2A, a) and, third, medium green regions appear to be enclosed within the reticulum (Fig. 2A, b). Each of these three patterns can be inspected separately.

In the 5-mm long melon a ring of about a dozen large, evenly spaced vascular bundles run longitudinally and directly beneath the dark green reticular surface regions, indicating some causal relationship exists between locations of vascular bundles and stripes (Fig. 2B, arrows). It seems that the vascular bundles collectively are a prepattern that determines the pattern of dark green reticulated stripes on a light green background. This stripping is also found on the pedicel, or flower stalk (Fig. 1B, arrow), indicating the prepattern and pattern exist prior to flower formation and is only fully expressed in an enlarging melon.

The complex reticulum of a stripe appears to be a set of polygons (Fig. 2A). The often incomplete but contiguous polygons seem to be cell clones for three reasons. First, these heavy outlined polygons are contiguous and not separated by spaces as in animal hair ([Meinhardt, 1976](#)). Second, these polygons are often found in pairs of equal sized polygons (Fig. 2A, c1 and c2) and sometimes in orthogonally arranged tetrads (Fig. 2C) as are found in daughter cells (Fig. 2D). The third argument for a polygonal array is as follows. The dark green reticulum is about 30 cells wide (Fig. 2A, a) and the central medium green region with fewer chloroplasts per cell has an average diameter of about 80 cells (Fig. 2A, b). Together they form a unit that if taken as a polygon averages six sides so the

number of cells in a polygon is about $d/2 \times d/4 \times 6$ or $110/2 \times 110/4 \times 6$ or about 9075 cells. This pattern is first observed in fruits with a 5-mm long major axis or with a circumference of the minor axis of 9.4 mm which later attains a length of 510 mm or a circumference of the minor axis at maturity of 650 mm for a 650/9.4, or 69.0-fold increase in circumference of the fruit. The typical polygon is bordered by a reticulum of about 30 cells in width and internally is about 80 cells in diameter. The diameter of the proposed polygon is then half the width of the reticulum, 30/2 or 15, plus the internal diameter of 80 plus half the reticulum width on the opposite side for a diameter of 15 + 80 + 15, or 110 cells. The initial number of cells of a polygon is then 110 cells/69.0-fold increase, or 1.60 cells. Generally, reticulation comes from individual cells each of which proliferates into a clone with a polygonal outline (Figs. 1G–I, 2D).

The medium green regions appear to be derived from the polygons, or cell clones. These regions are only found within polygons as polygons are not bordered on their outside by medium green regions but by light green background regions (Fig. 2A, d). Also, the centers of large polygons are often occupied by light green regions (Fig. 2A, d) as though the medium green regions extend from the reticular lines, or marginal cells of clones, only so far inward.

The question arises as to the best hypothesis that explains the presence of polygons. I have suggested that any proposed hypothesis is associated with a particular number of cells that should match the number in the data ([Korn, 2006](#)). The initial polygon is calculated to be less than two cell size which proliferates into a clone of about 9000 cells of three types according to intensity of color. That an initial cell gives rise to a clone of various types of cells suggests the clonal mosaic model of [Walter et al. \(1998\)](#).

The data supporting an initial cell giving rise to a many-celled polygon does not agree with what is expected for a reaction–diffusion mechanism. A reaction–diffusion mechanism requires a diameter of one induced region and at least two regions of inhibition, one on either side of the induced region, or initial polygons of about three regions in diameter. [Meinhardt's \(1976, Fig. 5A\)](#) illustration has a minimum of about six cells between induced peaks, unlike the minimum of one to two calculated here for the initial polygon. The clonal hypothesis, however, is acceptable as each initial cell can produce various types of cells according to their relationship to cell walls of the initial cell.

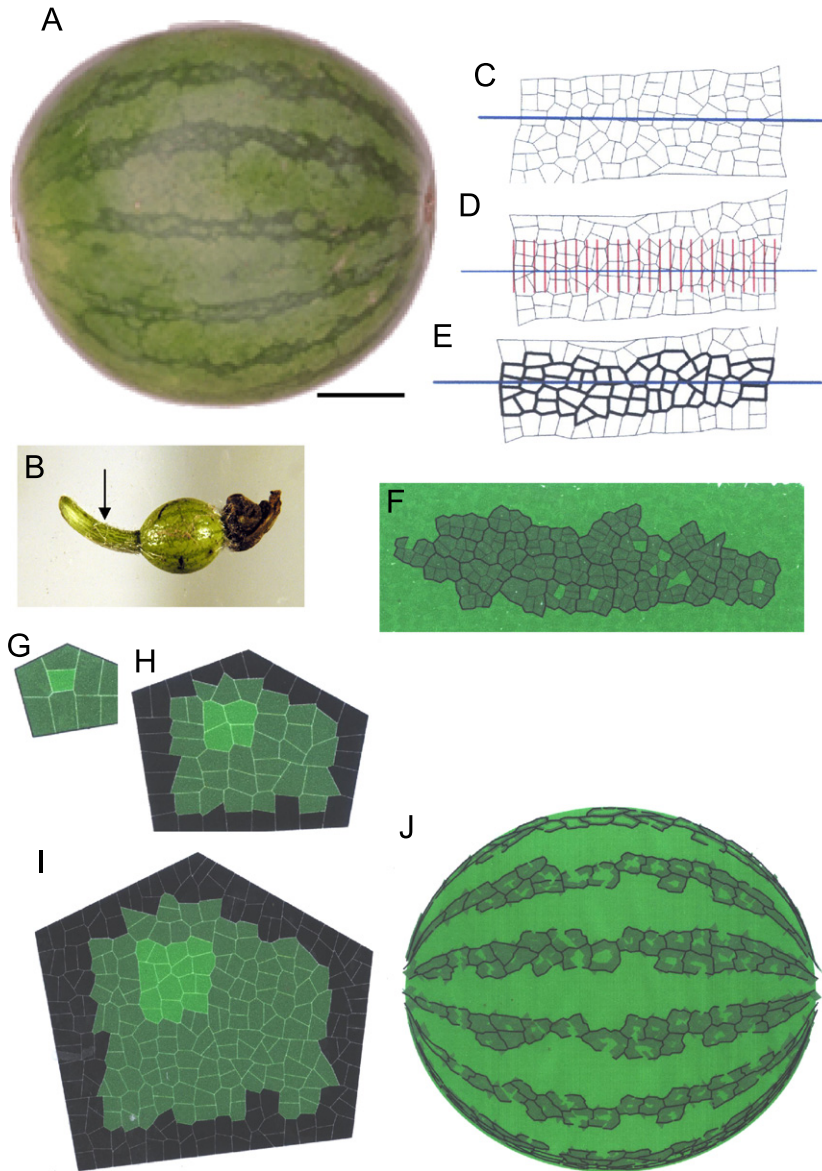


Fig. 1. (A) Mature Ruby Red watermelon with alternating light and dark green stripes. Bar is 5.0 cm. (B) A 5.0-mm melon already having stripes which can be traced back to stripes on the pedicel (arrow). (C) Computer drawing of initial state of a field of cells (black walls) and vascular bundle (blue line). (D) Computer depiction of first stage in which morphogen (red) diffuses from vascular bundle to cells. (E) First stage completed when model of cells differentiate (heavy black walls) within morphogenetic field. (F) Second stage in which cells with original walls (heavy black lines) induce cells to produce medium green condition. (G) Close up of second stage. (H) Third stage, after some proliferation, walls from initial cell induce their now resident cells to have dark green condition. (I) Final, fifth, state after more proliferation to have heavy green, medium green and light green (white) regions. (J) Watermelon at stage 3. Four groups of Figs. 2C–E, F, G–I and J are from different runs.

As noted above, the developmental sequence described here for watermelon has the important features of the clonal mosaic model for animal coat patterns developed by Walter et al. (1998). While a stripe in watermelon is a collection of contiguous polygonal clones with heavily pigmented marginal cells, the model of a giraffe's coat can also be seen as a collection of clonal polygons with all but their margins pigmented. (It can also be interpreted by a reaction–diffusion model [Murray, 2002].) The differences between the clonal mosaic model for animal coats and fruit stripping are only superficial. For example, cells of a clone in the animal model can migrate anisotropically and at

specific rates resulting in a particular pattern and in plants the same pattern arises by regional cell differentiation and these regions can recede from the clone center anisotropically not by migration as for animal cells but by cell proliferation. Another superficial similarity between animal and plant clones is the presence of 3 colors.

A computer model was constructed with the following features in order to test these assumptions. The model begins with a vascular strand and an overlying field of hypodermal cells (Fig. 1C). The first developmental step is that cells at least d distance from the vascular bundle (Fig. 1D) become clonal initials (Fig. 2E). The second

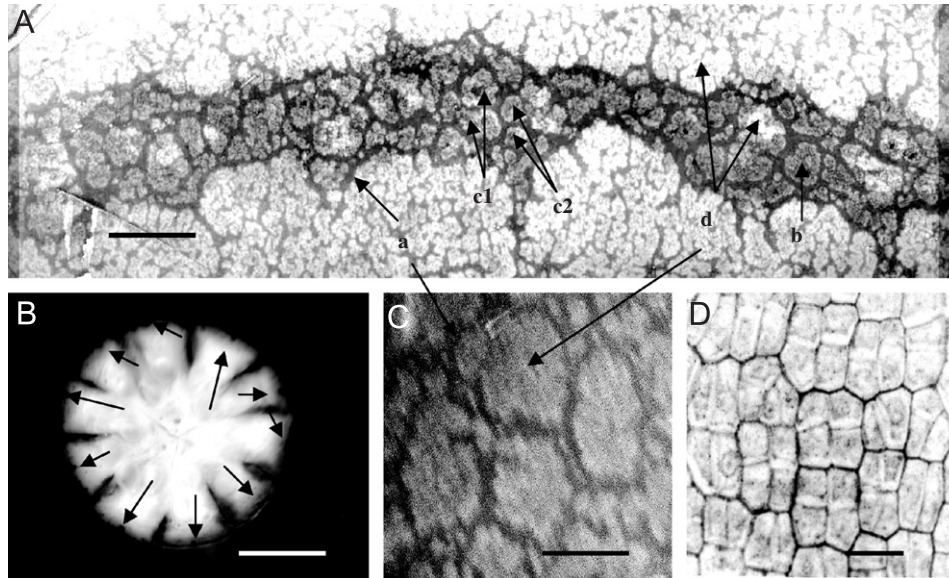


Fig. 2. (A) Stripe with reticulated dark lines (a), medium green shading in reticulated polygons (b), two pairs of polygons (c1 and c2) and light green central region (d). Bar is 6 mm. (B) Section of 5-mm melon with vascular bundle (arrows) between slits cut in light green background between stripes. (C) Four polygons in a reticulated region of a mature melon. Bar is 4.0 mm. (D) Cell arrangement in top epidermis of the *Aponogeton* leaf (Korn, 1980). Bar is 40 μ m.

developmental step is that each of these cells proliferates for about three cell cycles into a clone and the third step is that marginal cells become medium green cells (Fig. 1F, G). Third, three more cell cycles of proliferation make more medium green cells and, again, marginal cells of the clone with original wall fragments of the initial cell become specialized into dark green cells (Fig. 1H, J). Growth during steps 2 and 3 is less at the ends where the melon is attached to the constraining pedicel and old floral parts leading to a lens-shaped stripe (Fig. 1F). The rate of growth is a function of the distance from the ends, $k = r \sin(dl/d)$ where r is the uniform growth rate, dl the distance from the closer end and d the half length of the melon. Fourth, cell proliferation continues in the model for another two generations to give three types of regions, dark green reticulated areas, medium green areas within polygons and in some polygons a light green region near the center (Fig. 1I). The actual final polygons were calculated to have about 9000 cells, far more than what can be modeled, but model polygons of about 225 cells have the requisite three types of regions (Fig. 1I).

The Ruby Red cultivar studied here has distinct reticular stripes, more so than found in other watermelon cultivars

where this pattern can be identified only with great difficulty.

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