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# Vegetative development

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# 10

## OM10.1 CLONAL ANALYSIS

Clonal analysis has been used extensively to determine how the descendants of a particular cell or group of cells contribute to development. This process involves “tagging” individual cells with a specific phenotypic marker, which can be achieved using a variety of strategies. Endogenous transposons have been exploited in some plants, in which their excision from a gene in single cells changes the appearance of that cell and its descendants. For example, excision of a transposon from a gene involved in pigment production in maize kernels, resulting in restoration of pigment production in that cell, allowed the fates of its descendants to be followed through kernel development (see Section 2.2 and Figure 2.13). Other means of tagging individual cells involve the introduction of transgenes designed to mark individual cells at random with easily visualized **reporter genes**, and exposure of germinating seeds to mutagenic radiation treatment followed by screening of leaves for rare albino cells mutated in genes involved in chlorophyll production: the fate of descendants of these cells can be tracked because they also lack chlorophyll.

As described in the text, the shoot meristem of angiosperms is made up of distinct cell layers (L1, L2, and L3). The L1 (outer) and L2 cell layers are usually maintained as discrete single-cell layers as a result of their controlled, anticlinal cell division planes. Occasionally cells in one layer carry an albino mutation. Clonal analysis then shows how the descendants of a specific meristem layer contribute to, for example, leaf development, because the descendant cells also give rise to albino cells, creating clonal sectors (**Figure OM10.1-1**). Occasionally, cells originating in the L1 or L2 layer become displaced into one of the other cell layers as a result of an aberrant periclinal (rather than an anticlinal) cell division, creating a so-called “periclinal chimera.” If displaced cells are albino, they can again be used to observe clonal sectors and infer the underlying pattern of cell division and differentiation in tissue or organ development.

Clonal analysis has provided important information on how cell division is regulated to build the different organs of a plant and on the question of whether differentiation depends on a cell’s lineage or position – in the case of plants the answer is in most cases cell position.



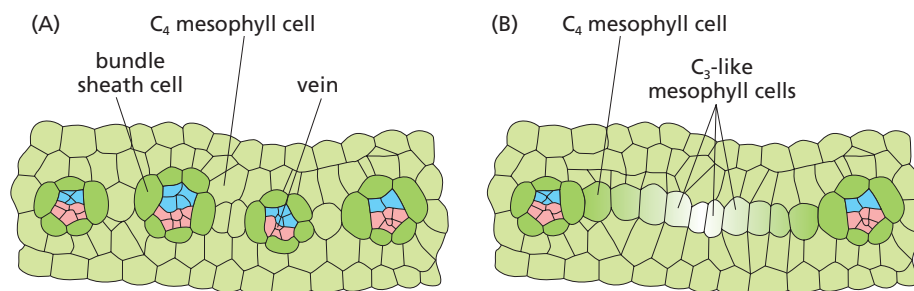
**Figure OM10.1-1 Albino and green sectors in *Ficus* leaves.**

These leaves were produced by a single plant in which the L2 layer of the meristem consisted of cells unable to produce chloroplasts (albino mutant cells). The green color of the leaves is due to the L3 layer, which gives rise to the spongy mesophyll and an inner layer of palisade mesophyll across most of the leaf. The edges of the leaves are albino because in these regions most of the mesophyll consists of L2 rather than L3 cells. (The L1 cell layer forms the outer layer on the adaxial and abaxial surface of the leaf but it is non-photosynthetic.) The differences between leaves in the width of the albino margin reflect relative contributions of the L2 and L3 layer to the mesophyll. The large albino sector in the leaf on the right (arrow) probably arises from the formation of a periclinal chimera early in leaf development, in which the L3 layer in the leaf primordium was “invaded” by descendants of the albino L2 layer.

## OM10.2 DEVELOPMENT OF C<sub>4</sub> LEAF ANATOMY

The leaf veins of C<sub>4</sub> monocots are surrounded by an inner cylinder of bundle-sheath cells and an outer layer of mesophyll cells. Both cell types have specific roles in C<sub>4</sub> photosynthesis that differ from the roles of photosynthetic cells in C<sub>3</sub> leaves. Veins in C<sub>4</sub> monocot leaves are very closely spaced: there are usually only two layers of mesophyll cells between veins (**Figure OM10.2-1A**). In C<sub>3</sub> leaves there may be ten or more photosynthetic cells between the veins. It appears that vascular strands are formed over a longer period of leaf development in C<sub>4</sub> than in C<sub>3</sub> leaf development. In C<sub>4</sub> leaves, new vascular strands continue to form between early-forming strands until the region between the strands is fully occupied by veins and their concentric rings of photosynthetic cells, whereas in C<sub>3</sub> leaves regions between early-forming strands are occupied by mesophyll cells that are not organized around veins.

The concentric arrangement of photosynthetic cells around the veins is essential for the operation of C<sub>4</sub> photosynthesis. In the photosynthetic husks of maize, early-forming strands acquire the typical C<sub>4</sub> concentric arrangement of photosynthetic cells, but - unlike the maize leaf - strand formation does not continue and the regions between veins with C<sub>4</sub>-like anatomy are occupied by photosynthetic cells with metabolism similar to those of C<sub>3</sub> mesophyll cells (**Figure OM10.2-1B**). Understanding the mechanism of formation of veins and their associated concentric rings of cells is a central goal of research directed at the introduction of C<sub>4</sub> photosynthesis into C<sub>3</sub> crop plants (see Section 4.5).



**Figure OM10.2-1 Vein positioning in a C<sub>4</sub> leaf.** (A) Each vein is surrounded by concentric layers of specialized bundle-sheath and mesophyll cells (an arrangement known as Kranz anatomy). Veins are thus separated by two mesophyll cells, whereas veins in C<sub>3</sub> leaves may be separated by ten or more mesophyll cells. Vein density is thus much greater in a C<sub>4</sub> than in a C<sub>3</sub> leaf. (B) In the photosynthetic husks that surround developing cobs of the C<sub>4</sub> grass maize, cells are arranged concentrically around the veins as in the leaf, but there may be ten or more mesophyll cells between these Kranz-like veins. Mesophyll cells that are distant from the veins have C<sub>3</sub> metabolism rather than the specialized metabolism of C<sub>4</sub> mesophyll cells.